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FURTHER STUDIES ON THE ACTIVITIES OF ARANEADS[1]

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1. AGE DIFFERENCES IN THE SNARES OF TWO ARGIOPIDS

To the best of my knowledge there has been made no comparison of the snares of immature and adult spiders, with regard to the problem of whether such snares become more complex as the animal grows older. Yet this is an interesting question in its bearings upon the perfection of an activity through repeated effort.

During the past months of July and August I have studied this matter on two common species of argiopids, *Epeira sclopetaria* (Clerck) and *E. marmorea* (Clerck), both of which construct large vertical, orbicular snares that are very favorable for measurements and the architecture of which has been well described by McCook.[2]

My observations were made at Woods Hole, Mass., where there was a large colony of *sclopetaria* in the laboratory buildings and beneath the boat wharves, and another of *marmorea* in a marshy woodland. All the webs measured were those in the free and natural conditions, except those of the newly hatched; to obtain the latter I kept cocoons until they hatched, then freed the young upon the window panes of my room where they spun their first snares. *Sclopetaria* makes cocoons throughout

[1] Contributions from the Zoological Laboratory of the University of Pennsylvania.

[2] American Spiders and their Spinning Work, Philadelphia, 1889–93.

the summer, and one female under observation furnished four successive ones (all made in the night); they hatch on the twenty-fifth or twenty-sixth day. *Marmorea* does not construct cocoons until the fall. Comparisons were made on the following points: (1) number of radii, (2) number of spiral loops, (3) greatest diameter of the spiral (orb proper). The spiral loops examined are those of the outer viscid spiral which is the true trap of the web, and the number of its turns were counted in that segment of the orb where they were most numerous (generally in the region below the central hub). A slight error is sometimes encountered in counting these loops for occasionally the innermost of them are scarcely distinguishable from the inner non-viscid spiral, but this is an error of only small amount.

The following table gives in condensed form the measurements of 265 snares. On the left is entered the species, sex and age, the linear measurements are in centimeters, the remainder is self-explanatory.

	Radii			Spiral Loops			Snare Diameter		
	Number of Counts	Extreme Numbers	Average Number	Number of Counts	Extreme Numbers	Average Number	Number of Counts	Extreme Sizes	Average Size
E. marmorea:									
♀ ♀, adult	87	19–43	28.3	87	29–71	48.2	86	18.5–48.3	28
♀ ♀, penultimate instar	19	21–35	27.8	19	16–61	48	19	16.5–35.6	23.4
♂ ♂, penultimate instar	16	23–36	28.3	16	26–61	41.3	16	14 –30	20.6
♂ ♂, antepenultimate instar	3	19–34	27.3	3	37–39	38	3	19.6–25.4	22.1
Young from .3–.6 cm.	23	19–35	28.7	23	16–51	29.5	21	7.6–28	15
E. sclopetaria:									
♀ ♀, adult	24	15–24	19	21	26–56	35.4	24	24.1–48.3	35.6
♂ ♂, penultimate instar	2	18–23	20.5	2	24–30	27	2	20.3–30.5	25.4
Newly hatched	91	11–20	15.3	91	11–23	16.2	91	5.1–11.9	7.6

With regard to increase of complexity of the snare with advance of age of the spider this table shows us the following figures for *sclopetaria.* The first formed snares, those of the newly hatched, exhibit an average of 15.3 radii, 16.2 spiral turns and 7.6 cm. diameter in comparison with averages of 19. radii, 35.4 spiral turns

and 35.6 cm. diameter of adult females. In other words while the diameter of the orb increases nearly five times, the number of spirals becomes slightly more than doubled, and the number of radii are increased less than one quarter. For *E. marmorea* the webs of immature individuals of from .3 to .6 cm. were compared with those of adult females, and the table shows that between these ages the number of radii remains about constant, while the number of spiral turns and the diameter of the spiral about double themselves; females in the penultimate instar show the orb almost as complex as that of females in the last instar.[3] For both of the species examined, accordingly, the age changes in the snare are greatest with regard to the diameter of the viscid spiral, less with regard to the number of its loops (on the average these only doubling their number), and least with regard to the number of the radii.

It is interesting that the first snare of the spiderling has all the parts of that of the adult, namely, the central woven hub and the inner non-viscid spiral in addition to the viscid spiral, radii and foundation lines. With increasing age of the spider the threads of the snare become thicker, the whole structure larger, but otherwise beyond the addition of a few more radii and a doubling of the number of the spiral turns there is no particular change effected. The newly-hatched show also about the same specific habits as do the adult: in *marmorea* the young, as does the mother, remains in a nest in a curled leaf holding communication with the snare only by a trap-line; and in *sclopetaria* the young, again like the mother, remains either at the center of the snare or else away from it, holding a trap-line but not hiding within a nest. Further, though there are frequently imperfections in the snares of the young, such as incomplete radii, asymmetri-

[3] By last or ultimate instar is meant the one of sexual maturity, even though this may be, and in some species regularly is, followed by other moults; the penultimate instar would be the next preceding, and the antepenultimate the one before that.

cally placed spirals and imperfect meshing of the hub, such imperfections seem to be quite as usual in adult webs so that it is rare in either of these species to find perfectly symmetrical webs. The adult spider can not be said to construct a more serviceable snare than does the spiderling, for the spiderling's is really much larger in diameter in proportion to the size of the body. And while the adult has about twice as many spiral loops, the spiderling with his fewer loops probably secures all necessary nourishment to the same extent as does his mother. Thus with the growth of the spider the snare does not become more serviceable as a trap. In all this excellent architecture the young as well as the adult labors first to make a scaffolding to support its weight, then lays down upon this the food-gathering spiral; and it does this quite as efficiently as does the adult. We might conclude that the number of spiral loops becomes larger because the supply of available silk has greatly increased; and that more radii are added because the weight of the spider increases faster than the size of the web, and because the spider in all her building tests the strength of the scaffolding, adding a new line wherever the structure sags. But the increase in number of parts can not be ascribed to intelligence, or memory of reiterated experience, for the mother seems to continue the same instinct possessed by the young and shows no peculiarity in the spinning process not exhibited by the latter. The age differences of the web are, accordingly, due mainly to: (1) increase in the weight of the spider in combination with the instinct to make the scaffolding sufficiently strong; and increase of size of the spinning organs, therefore of silk substance. The spider does not exhibit learning at any stage, for it constructs the first web with as much ease and certainty as any later one. In this connection I may also mention, as the result of many observations, that the spider makes the first cocoon as perfectly as any subsequent cocoon; and when it makes a mistake at any part of the process of cocoon spinning seems unable to rectify it.

The absolute size of the snare and the number of spiral loops vary much in individuals of the same species. The size is dependent upon two factors: (1) size of the space in which the web is spun, and (2) amount of silk available. If confined in a cramped place the spider spins no snare at all, as I found by attempting to induce them to spin in cages made of two panes of window glass separated by a wooden rim 3 cm. thick. Then if successive webs are destroyed soon after making each contains fewer parts than its predecessor, which can be ascribed only to deficiency of silk. Thus with one adult female of *sclopetaria* her first snare had 21 radii, 35 spiral loops, and a diameter of 37 cm.; this I destroyed, and her second made a day or two later had 17 radii, 25 spiral loops and a diameter of 30.5 cm.; a week later I destroyed this and she made a third with 18 radii, 25 spiral loops and diameter of 24.1 cm., then (after demolition of this one) a fourth with 19 radii, 19 spirals and diameter of 23 cm.

In orbs of adult females, particularly of *marmorea,* the space between neighboring spiral loops varies greatly in size, whence it follows that the diameter of the orb is no index of the number of spiral turnings, and that different females must use different parts of the body as a measure of this space. This is really the most marked variation to be found in orbs, and it is shown just as well in those of spiderings.

2. The Snares of Male Argiopids and the Number of Males

In this conjunction I wished to compare the spinning activities of males of *Epeira marmorea* and *E. sclopetaria* with those of their females. On this matter McCook has to say:[4]

> As a rule, the spinning abilities of male spiders, as far as they relate to the capture of prey, have been shown in Volume I to be less decided than with females. The rule is not absolute for all species, as in some cases the snare spun by the male is precisely like that woven by

[4] *L. c.*, 2, p. 65.

the female. But in certain other genera, as, for example, Argiope and probably Nephila, the snares of the male are rudimentary, and do not compare in perfection with those of the female.

The immature males of the two species studied by me construct perfect snares of the types of those of their respective females. But the adult males of *marmorea* (no adult males of *sclopetaria* were examined) do not spin snares at all but build nests near those of adult females and live on the outskirts of the snares of the latter; this was the case with all of the 23 mature males found in the latter half of the month of August.

Data on the snares of immature males are condensed in the table already presented. The snares of orbs of 16 males of *marmorea* in the penultimate instar show the same average number of radii, a somewhat smaller average number of spiral loops (41.3 to 48), and a smaller average diameter (20.6 cm. in comparison with 23.4 cm. and 28. cm., as compared with snares of females of this species in the penultimate instar and at maturity. Data for the snares of 3 males in the antepenultimate instar show somewhat lower averages. Those of 2 males of *sclopetaria* in the penultimate instar, show, on comparison with adult females of this species, a slightly greater average number of radii (20.5 to 19), a smaller average of spiral turns (27 to 35.4), and a smaller average diameter (25.4 cm. to 35.6 cm.). That is to say, males in their penultimate instar construct fully as many radii as do females in their penultimate or even ultimate instar, but a smaller number of spiral turns and they make smaller snares. But a male in his penultimate instar is considerably smaller than a female of the same age, therefore in proportion to his size and weight his snare is quite as complicated as that of the female and is in no sense rudimentary. It would appear, accordingly, that the spinning instinct, so far as the snare is concerned, is as perfect in the male as in the female. He makes no web when mature because the sexual impulse completely overcomes the desire for food, hence the instinct for snaring it, though

he does continue to construct nests; and his nest is quite as complex as that of the female. I have not determined whether a male after satisfaction of his sexual desires would again spin a snare; but probably he would not have a chance of doing so, for the female becomes satisfied before he does and frequently succeeds in devouring him. Indeed, I have obsrved a female of *marmorea* devouring one male while another was importunely making advances to her.

As to the sexual ratio of *mormorea,* I found in the field 16 males of the penultimate instar to 19 females of the same age, and 23 adult males to 87 adult females. These figures are too meager to allow of any general conclusion, beyond that the males at maturity seem to be less than half as numerous as females, and just before maturity to be slightly less numerous. The greater disparity in numbers at maturity may well be due to accidents befalling males while they are seeking mates and to their destruction by the females themselves. On August 31 I measured the orbs of 24 adult females of *marmorea;* on only 8 of them were there adult males, these webs having from one to three males each. It is probable that more than one male copulates with a given female, and that a given male may mate with more than one female; for I have found this to be the case with *Theridium tepidariorm* and certain Lycosids.[5]

3. The Senses of Touch and Sight in Snare-making Spiders

The number of eyes in araneads, usually eight, their different positions upon the head area, and their complexity in being compound (constructed of separate retinulae), has led naturalists to the view that the sense of sight plays a large part in their vital activities. And this idea is substantiated for such species as are strictly hunt-

[5] Before the antepenultimate instar males can not be distinguished externally from females. According to W. Wagner (La Mue des Araignées, *Ann. Sci. Nat.,* 1888) the external male peculiarities do not exhibit themselves in *Attus* before the fifth moult, and in *Lycosa* before the seventh.

ers and not snarers, and particularly for the diurnal Attidae as demonstrated by the studies of the Peckhams.[6] But among the snare-weavers I feel positive, in agreement with McCook's conclusions, that the sense of touch almost completely supplants that of sight. Long observation in the field and especially upon species kept under control has led me to this opinion, the main reasons for which may be briefly mentioned. The lines of the snare are the medium by which the spider secures its food and conducts its mating, all by touch. In the operation of spinning, whether it be a snare or a nest or a cocoon, the process is conducted beneath the ventral surface of the spider, accordingly, in a position removed from its field of vision; and all such architecture is frequently carried on in the dark of night. With the true orb-weavers, the argiopids, the spider sometimes remains at the center of the orb holding tensely with its tarsal claws various radii and thereby feeling any object that strikes the web. In this position she can see only a small part of the snare, if any of it, yet she instantly perceives any impact upon any part of the snare. Or the spider does not rest upon the snare at all, or comes out upon it only at night and twilight, remaining in a nest at some distance from the snare; in that case the spider perceives any shock to the snare by means of the trap-line that passes from her claws to the center of the snare, such a trap-line being a modified radius. McCook (*l. c.*) has given an admirable treatment of the use of this trap-line and of how it is often employed to spring the snare. Thus *Epeira marmorea* remains through the hours of sunshine for the most part in a nest within a leaf that has curled up, where she can not see the web at all, and feels every motion of it through the connecting trap-line. And it is instructive to watch her when an insect agitates the snare. She then rapidly pulls the trap-line several times, thereby learning that the prey is struggling in the web, runs

[6] Peckham, G. W. and E. G. Sense of Sight in Spiders. *Trans. Wisconsin Acad. Sci.*, 1894.

rapidly to the center of the snare, then locates the insect precisely by pulling successively different radii. In this food-gathering she seems to use touch alone, and it is questionable whether she at any time sees her food, for even in the process of mastication and sucking she holds it beneath her head. And this sense of touch is so delicate that by it the spider can to some extent determine the nature of the object that causes the impact, as, *e. g.*, whether it be large or small.

Likewise with the mating, that I observed this summer in *Epeira marmorea*. The female was near the center of her snare hanging vertically downward with her dorsal surface, her vision area, away from the male. He was at the outer end of one of her radii and though his head was turned towards her he perceived her position and tested her inclinations not by sight but by touch communicated through that radius; they signalled to each other by pulls and counter pulls of the line, he climbed along the radius towards her, at nearly every step repeating his pulling, then when about an inch away he advanced rapidly to press his palpi against her epigynum while she drew in her extremities close to her body. Each such act was only of momentary duration, and at its end he moved away along the same radius, repeated his signalling, then again advanced towards her; thus there were numerous repeated copulations during the half hour I watched the pair.[7] The female never saw the male at all, and he perceived her so far as I could determine by the sense of touch alone. In an earlier study, where I

[7] Previous observers of European species of this genus have described this process in much the same way. Compare:

Walckenaer. Histoire naturelle des Insectes. Aptères. Suites à Buffon, 2, Paris, 1837.

Menge, A. Ueber die Lebensweise der Arachniden. *Schriften naturf. Ges. Danzig*, 4, 1843.

Menge. Preussische Spinnen, I. *Ibid.* (N. F.), 1, 1866.

Termeyer, R. M. de. Researches and Experiments upon Silk from Spiders, etc. Translated by Burt G. Wilder, *Proc. Essex Inst.*, 5, 1866.

Lendl, A. Ueber die Begattung der gekrönten Kreuzspinne (*Epeira diadematа* Cl.). *Termész. Fuzetek, Budapest*, 10, 1886.

described this act in much greater detail for various other species,[8] I had called attention to this exclusive use of touch in the courtship and copulation of snare-weavers. The female responds to the male's signals by more gentle and weak pulls when she is eager for him, by stronger and more aggressive ones when she regards him as an object of food; thus there is a language of touch, even at a distance, and the male assures himself, if such an expression is permissible, of the nature of his partner's responses. In the case of *marmorea* just described the male took effective means to procure his escape should the female prove aggressive, just as did the male of *E. diadematа* observed by Menge: while advancing along her web radius he held an escape line of his own, the outer end of which was attached to the periphery of her web; and when her motions were more violent than usual he loosed his hold on her radius to drop and swing out of her reach on his own escape line. In this way he procured the double advantage of escape and of remaining in communication with her web.

It may be noted in passing that while in *E. marmorea* the male seeks only adult females, in *Theridium tepidariorum* the males mature somewhat earlier than the females and are to be found upon the webs of the females before the latter have matured.

We can say that among araneads the sense of touch is the dominant one in those that are snarers. Spiders lack hearing, as seems to be proved by the experiments of my student Miss Pritchett.[9] The long spines placed upon the limbs seem to be tactile and not auditory organs. Spiders possess the olfactory sense but it is not known how much they are guided by it. The primary sense of the snarers is touch, and they possess it to a

[8] Studies on the Habits of Spiders, particularly those of the Mating Period, *Proc. Acad. Nat. Sci. Philadelphia*, 1903.

[9] Pritchett, A. H. Observations on Hearing and Smell in Spiders. AMER. NAT., 38, 1904. These observations have been criticized by F. Dahl (*Naturwiss. Wochenschr.*, N. F., 4, 1905), but Dahl never instituted crucial experiments such as those of Miss Pritchett.

degree of perfection hardly equalled by any other terrestrial animals.

The question then presses, of what use are the eyes to snare-weavers when their sensations are so particularly tactile? The newly hatched spiderlings evidently use their eyes for they are always positively phototropic while the adults are generally negatively so. This turning towards the light benefits the spiderlings and consequently the species by serving to disseminate them from the home area into new feeding grounds. And I believe it is a quite general phenomenon among all animals whose adults are more or less sedentary and tubicolous, negatively phototropic, for the young to be at first positively phototropic, though I do not know whether any one has drawn attention to the comprehensiveness of this principle; in this most wide-spread kind of migration the beneficial result of the change of tropism is to prevent overcrowding. But as the young snare-weaver grows older and begins to avoid the light as does its parent, it does not employ its eyes in the primal acts of feeding and mating but mainly determines by them the source of the light in order to avoid it. Despite their complexity, accordingly, the eyes of snare-weavers, when they have passed infancy, seem to be used mostly as direction eyes. This being the case it seems strange that these eyes should have retained the complexity inherited from hunting forefathers, and it is possible that they have come to subserve some other new function, as, *e. g.,* to have become thermic receptors; this might well be determined experimentally. At any rate we shall have to change current views as to the rôle of vision in spiders.

4. On the Average Duration of Life in Araneads

In the case of all species that I have studied adult males are found during only a short period of the year, for perhaps not longer than a month or six weeks, and in latitudes where there is a marked winter season they do not live over this period of cold. And from observations on *Theridium tepidariorum* I estimate from the rate

of growth that this species is able to reach full size in one year. Males, accordingly, live for only a relatively short time as adults, and their life time would seem to not exceed one year. In my observations on *Epeira marmorea* I found on July 25 among 16 recognizable females (in young of 8 mm. body length or less the sexes are externally indistinguishable) only 5 adults, while on August 31 out of 24 females all but 3 were adult; these data indicate for this species that while at the beginning of the summer few females are adults, at its end most are. It is then probable for this species, though not proved, that few females live over from one breeding season to another, and then only under favoring environmental conditions, a conclusion reached by McCook for *Argiope*. But the females live at least some months longer than the males for they are to be found later than the breeding season and after all males have disappeared; and there are cases on record (cf. McCook) where females of certain species have been kept from two to seven years. I have described for *Latrodectus*[10] how the mating occurs in the late winter at Austin, Texas, the adult males are not found after this season, while the females continue to produce cocoons until the following autumn. We might say in general that males of spiders probably do not live longer than one year, females some months longer or in certain cases several years.

5. The Cocooning of Loxosceles rufescens Duf

I give these brief notes here because the cocooning of no sicariid has been hitherto described, and because it may be of some interest from the standpoint of comparative architecture. The cocoon of *Loxosceles* is sessile, attached to the snare, so resembling that of *Sicarius*, while in *Scytodes*, the only other genus of the Sicariidae for which the cocoon has been described, it is carried in the chelicera of the mother.[11]

[10] *Jour. Exper. Zool.*, 5, 1908.

[11] I have taken these genera as defined by E. Simon: Histoire naturelle des Araignées, 2me éd., Paris, 1892.

This is an abundant form at Austin, Texas, where it makes a large and irregular web beneath logs and stones, usually in drier situations. In its movements it is the most languid and timid species I have ever seen, waiting quietly until its prey has inextricably entangled itself in the web, and feigning death for a remarkably long period. Both males and females are able to undergo thirst for weeks at a time, an unusual faculty among spiders, and to this ability it probably owes its success under the desiccating Texan sun.

On June 13, 1907, I placed six females in separate glass cages. Four of them when first found had each a single cocoon, and each produced cocoons in captivity to the number of from two to four each. One of them produced five cocoons in all.[12] The season of cocooning evidently extends through the whole three months of the summer.

The cocoons are discoidal, with diameter longer than the spider's body, and are made in the mornings from seven o'clock to noon. In the two cases where the operation was observed they were spun against a vertical wall of the cage, not placed horizontally. After making the base, a process not seen, the spider remains quietly above it until the following day, a cessation of activity quite unique among araneads but thoroughly in accord with *Loxosceles's* quiet disposition. Then the eggs are laid upon this base, an act that occupied eight minutes in the case where it was followed. Over the egg mass the mother spins a thin-textured cover, swaying the spinnerets leisurely back and forth; this cover spinning occupied one hour in the case where it was timed. The mother remains upon the cocoon until it hatches.

[12] Some naturalists write as though multiple cocoons were a rather exceptional phenomenon among spiders. On the contrary I believe it is the general if not universal rule, for I have found it to be the case also in lycosids, pisaurids, attids, agalenids, thomisids, clubionids, drassids, theridiids, argiopids, dictyniids and filistatids.

NOTES ON THE DAILY LIFE AND FOOD OF CAMBARUS BARTONIUS BARTONI[1]

FLOYD E. CHIDESTER

In all animals we find that there are periods of activity and rest. During the active period, we find such interesting phenomena as feeding, copulation, and, in some animals, a very interesting series of movements connected with the care of the young.

My study of the daily life of the crawfish is one of a series of studies instigated by Professor C. F. Hodge in the effort to arrive at some accurate data as to the work performed by various species.

Crawfish were kept in two different aquaria during the winter of 1907-'08, and their actions watched closely.

One tank was an ordinary running water tank with a pile of sand at one end, and containing, in addition to crawfish, at times, trout eggs, young trout, frogs, clams and a turtle. There were also, all the time the crawfish were kept there, several tufts of the common water weed, Fontinalis, floating in the water.

The other tank was a heavy glass aquarium, measuring on the inside, 1 x 1½ x 2 feet 8 in. This aquarium was elevated about an inch at one end, and beginning at the other end, a mud and sand bottom sloped gradually upward to a level bank which was covered with moss and grass and kept moist

In the aquarium was a clam to assist in clearing the water, a water hyacinth, and some more of the water weed mentioned above.

At different times, as I experimented with the food of the crawfish, there were bits of fresh meat, sprouts, eggs and young of trout, toads, frogs and salamanders; dead frogs and fish, and dead crawfish.

[1] Contributions from the Biological Laboratory, Clark University.

The water was changed daily and oftener at feeding time, during the entire winter, and record kept of the activities of the crawfish. It was not until spring, however, that night and day observations were made.

During the fall and winter, up to February 1, frequent cases of copulation were observed. Contrary to Dearborn's statement, '00, I found that the males do not know the females and that males repeatedly grasp other males, and sometimes, in spite of their frantic struggles, turn them over and attempt to copulate with them. The difference in behavior in the case of the male, when thus grasped, is that he continues to resist violently at intervals, until released, while the female, as soon as grasped firmly, ceases to struggle, and lies passive.

Another interesting thing was noted in connection with the actions of crawfish before moulting. In the case of adult crawfish with hard exo-skeletons, I found that for two or three days before the ecdysis, they would come up partly out of the water, so that the carapace was entirely out of the water, and dried out thoroughly.

Crawfish when transferred from the running water tank to the still water one, would almost immediately seek cover, generally burrowing into the bank, and remaining during the day with their heads toward the entrance, quiet unless disturbed.

In the still water aquarium, there were at one time, six crawfish hibernating in the bank, with their burrows stopped up, for three weeks. The other seven in this tank were in the deep water under plants during the day, but, as darkness fell, they came up into the shallows and on the bank.

Repeatedly, I have come into the building after darkness had set in, and seldom failed to find several crawfish on the bank.

Crawfish are generally supposed to be omnivorous. They are not, however, so fond of decayed matter as has been supposed. Tests made in the laboratory show that, when they refuse to eat stale food, they will eagerly con-

sume fresh. They will eat fish which have been recently killed, in preference to partly decayed ones.

In the spring, after moulting, there seems to be a consuming hunger. I have seen, at about 9 P. M., a crawfish within about six inches of the bank of a small pond, so intent on pulling to pieces and devouring a partly decayed fish, that he did not notice the very strong acetylene light that I held close to him.

Experiments with lights of various intensities, elucidated the fact that crawfish are negatively phototactic to strong light but positively phototactic to weak light.

Raw and cooked meat of all kinds, worms, dead fish, pieces of clam, moulting crawfish, and dead crawfish were eaten by the crawfish in confinement. They are said to eat their own cast-off coats, but although these were left in the aquarium for about a month, they were undisturbed.

Tests were made to determine if the crawfish would eat fish (trout), frog and toad eggs. Very few were eaten, and these few when the crawfish had had nothing to eat for ten days, and had nothing else to eat.

Young frog and toad tadpoles were kept in the aquaria and lived happily for a long time. To determine if crawfish eat toad or frog tadpoles, twenty-five toad and frog tadpoles were placed in a shallow dish, and, with a renewal of water every day, kept for four days with a single, supposedly hungry, crawfish. Of the twenty-five tadpoles, in all, but eight were eaten.

About two weeks later, when the tadpoles had become quite a little larger, a test was made with toad tadpoles. A male crawfish was placed in a shallow aquarium jar with twelve live tadpoles, and kept for three days, with change of water twice a day. It was not until about fifty hours had elapsed that he ate of the tadpoles, and then he ate but one.

A female crawfish was put into an aquarium jar at the same time as the male, with 12 live toad tadpoles. This was at 5 P. M. At 6 P. M., she had eaten all but one of them. At 6 P. M., 17 more were put in, making 18 in all.

At 10:30 P. M., five more tadpoles were gone. At 9 A. M., on Friday, only 5 were left, one of these being dead. This was a record of 22 out of 27 active tadpoles in 16 hours. The female was seen to catch several of the tadpoles, using for this, not her cumbersome chelæ, but her smaller, nimble, first pair of ambulatory appendages.

Evidently *Cambarus bartonius bartoni* is capable of catching toad tadpoles, but it is improbable that many are caught, for I am informed by Mr. Newton Miller that the young tadpoles, although near the shore during the day, go to the deeper water at night. It is at night that the crawfish come into the shallower water near the shore, and even part way out of the water. Here it is that they may catch an occasional fish, frog or toad.

Two young frogs were kept during the greater part of the winter in one of the aquaria on my desk with the crawfish, but none of the dozen seemed able to kill them. Once I forced a frog to swim down to one corner of the tank where several crawfish were collected, and one of the crawfish grasped a hind leg with his right chela, and a moment later secured the front leg on the same side with his left chela. He then forced the frog to the bottom and attempted to pull him limb from limb, all the time holding the animal under water. In just a moment, however, the frog kicked with his free hind leg, and accidentally striking the crawfish on the carapace, was released.

My observations and experiments in the laboratory were supplemented by many evenings spent on the shores of several small ponds near the university, observations being made by means of a strong acetylene light. I believe, in the light of these observations, that the crawfish in the still water aquarium behaved normally.

In the spring, the crawfish is very active, and feeds with much more eagerness than during the winter. It is then, too, that the interesting phase of the mother's care of the eggs may be best seen.

On account of this, I took occasion to watch a pair of crawfish, a male, and a female with eggs just about ready

to hatch, through 24 consecutive hours, beside several observations of lesser duration.

In these observations, I was aided by Dr. C. F. Hodge and Mr. Newton Miller, who kindly gave me occasional resting periods.

The first set of observations which I shall record were made on May 16–17, 1908.

Observation was begun at 6 P. M. on two crawfish, a male and a female with eggs about ready to hatch, and lasted until 6 A. M. the following day. In the aquarium with the crawfish, were the water hyacinth and Fontinalis mentioned above, some young sprouts, five young toad tadpoles, and some pieces of fresh meat.

The male was moderately active between 8.10 and 8.45 P. M., most active between 12. and 1.30 A. M., and had a lesser period of activity between 2.05 and 2.30 A. M. The longest period of quietude was from 1.30 to 2.10 A. M. He ascended and descended the bank nine times during the 12 hours. The male did not feed.

The female ascended and descended the bank 84 times during the 12 hours. She ascended and descended 17 times between 1 and 2 A. M. She would climb the bank and aerate her eggs in the open for several moments, then retire to the deep water and almost immediately return to the bank. The greatest activity was from 11 P. M. to 6 A. M. She fed at 6.50 and again at 7.07 P. M. both times on the fresh meat. Her longest rest period was from 10.30 to to 11 P. M.

The next series of observations was performed on three crawfish, the two observed on May 16–17, and in addition, a female without eggs. This time observation was kept up for 24 consecutive hours, from 1 P. M. May 19, to 1 P. M. May 20.

The same kind of food was used as before, care being taken to avoid fouling the water with it until about one-half hour before the records were taken.

The male fed a great deal this time on the fresh meat, feeding from 1.35–2.15 P. M., 2.30–245 P. M., 3.18–3.40 P.

M., 3.48–5.00 P. M., 4.10–4.30 P. M.

He was most active from 11.35. P. M. to 3.15. A. M. It is interesting to note that each period of feeding, if lengthy, was followed by a correspondingly long period of rest. The longest rest period was from 4.45 to 8.05 A. M. The male did not ascend the bank at all during the 24 hours.

The female with eggs began ascending the bank and aerating her eggs at 4 A. M. and stopped at about 4.25 A. M., then began again at 6.15 A. M. gradually lengthening the stay on the bank until 9 A. M. then shortening the frequency of the visits, and lengthening the stay in the water; this period of less frequent visits lasted until 11 A. M., then from 11 A. M. to 12 M., there was great regularity of aeration, and from 12 M. to 1 P. M., less frequent aeration. Ascent of the bank was made thirty-four times during the 24 hours.

Feeding was done at 1:45 P. M., and again at 2.15 P. M., but in neither case did it last longer than ten minutes.

Number seven, a female without eggs, was very inactive, staying under a stone the greater part of the time. She came out on the bank but three times. Her period of greatest activity was between 3.30 and 4.15 P. M.

From these observations of the crawfish in nature and in the laboratory, we may conclude as follows:

1. Crawfish are most active at night.
2. There is marked activity at nightfall and at daybreak.
3. Feeding is generally done at night, but may occur during the day.
4. In the spring, the crawfish eats much more often than during the winter.
5. *Cambarus bartonius bartoni* prefers fresh animal food to anything else.
6. Feeding is followed by rest, prolonged periods of feeding being followed by equally prolonged periods of rest, the animal not becoming active for several hours.
7. There is apparently no spontaneous play or exercise, movements being purely utilitarian.

8. A female aerates her eggs both on land and in water.

9. Crawfish come up into the shallows and elevate their carapaces partly out of the water.

10. Combing or cleaning movements are executed by means of the first and second ambulatory appendages. These consist in scraping the carapace.

11. Males do not distinguish between the other males and the females, and frequently grasp males and attempt to copulate with them.

LITERATURE

1895. Andrews, E. A. Conjugation in an American Crayfish. *Am. Nat.*, Vol. 29, pp. 867–875.

1900. Dearborn, G. N. Notes on the individual psycho-physiology of the crayfish. *Am. J. Physiol.*, Vol. 3, pp. 404–433.

1895. Herrick, F. H. The American Lobster. *Bull. U. S. Fish Commission*, 1895, pp. 1–252.

Ortmann, A. E. The Crawfishes of the State of Pennsylvania. *Memoirs of the Carnegie Museum*, Pittsburgh, Pa. Vol. 2, No. 10, pp. 343–523.

SOME POINTS IN THE ECOLOGY OF RECENT CRINOIDS

AUSTIN HOBART CLARK

ALTHOUGH a considerable amount of work has been done on the anatomy of various species of recent crinoids, the embryology and development of two species, closely allied, are well understood, and the systematic side of the question has received more or less attention, little has been accomplished in the elucidation of the interrelation of the crinoids and the other classes of marine invertebrates, or the relation of the crinoids to marine conditions in general. This is undoubtedly due to the rarity of the group, and its chiefly inaccessible habitat, rendering it, as a whole, a difficult subject for extensive research; but much may be learned from the data already recorded, and it is the purpose of the present paper to suggest certain lines along which much of interest may be done on the basis of the present numerous, though scattered, records.

It has long been known in regard to *Antedon bifida* of the coasts of Europe that specimens taken in deep water are larger than those taken in shallow water or along the shore, though no plausible reason has been shown for the phenomenon. It has been suggested that the coldness of the deeper water may stimulate it to greater development; but specimens from different localities, taken at a considerable difference in depth, yet with the same bottom temperature, will vary greatly, those from the greater depth being much the larger; similarly, specimens from the same depth, but with marked difference in the bottom temperature, will be found to be of practically the same size. As, however, specimens from very shallow water are usually about 120 mm. in expanse, while those from deep water are 220 mm. or more, it is evident that some important factor is involved.

The food of crinoids consists of very small pelagic organisms and minute crustacea. At or near the surface the crinoid must depend upon those which swim within reach of its pinnules or which it may intercept by the slow movement of its arms; but in deeper water while this source of supply is just as available as at the surface, the crinoid gets, in addition, all the carcasses of those organisms in the levels above it which die and are precipitated to the bottom. The intensity of this rain of food increases proportionately with the depth, so that the deeper a crinoid lives, the greater is the available food supply; consequently, the better nourished will be the individual and the greater its size.

We see, therefore, that the size of *Antedon bifida* appears to be merely a question of food supply. Passing from a single species to a consideration of the group in general, we find that the average size gradually increases from the shore line to about the 100 fathom mark; this is plainly due to the gradual increase in the supply of food, as just explained; from 100 fathoms to about 600 fathoms the same size is maintained; but below 100 fathoms plant life, and with it the host of small organisms dependent directly or indirectly upon it, upon which (as well as upon certain of the minute plants) crinoids are dependent for food, begins to disappear. This gradual disappearance of vegetable organisms and their dependents is offset by the gradual increase in the rain of carcasses from above, so that an equilibrium is maintained down to about 600 fathoms, and hence the size of the crinoids remains about the same from the 100 to the 600 fathom mark. Below 600 fathoms, the gradual decomposition of the rain of carcasses progressively lessens its food value, and, therefore, we note a decrease in the size of the crinoids, hardly noticeable at first, but soon becoming more marked, until, below 2,000 fathoms, we find only the minute comatulid Bathymetra and the equally minute stalked Bathycrinus.

By this hypothesis the general absence of the Pen-

tacrinitidæ above 100 fathoms is at once explained; the stalked pentacrinites (Encrinus, Endoxocrinus and Hypalocrinus) are animals of very considerable size; besides a large crown they have a bulky stem which must be nourished, and the organisms found at or near the surface are not sufficient to support them; it is not until the depth of approximately 100 fathoms is reached that the organisms occurring in the water about them, plus the cumulative effect of the rain of dead from a belt 100 fathoms in depth, acquires sufficient intensity to admit of their existence. Incidentally, their remarkable uniformity in size is explained; for the recent pentacrinites inhabit almost exclusively the 100–600 fathom belt, which has just been shown to be a belt of uniform crinoid size. A species of Endoxocrinus, *E. wyville-thomsoni,* and the peculiar Hypalocrinus both descend to over 1,000 fathoms, but both are much smaller than their relatives above the 600 fathom line.

The common arctic comatulid, *Heliometra glacialis* (= *eschrichtii*) occurs from east of the Kara Sea to westward of Greenland, thence southward to off Nova Scotia;[1] the southern part of the Sea of Okhotsk and the northern part of the Sea of Japan are inhabited by a variety, *maxima,* differing only in its great size. This species varies greatly throughout its wide range; north of Europe it is small, though rather larger around Spitzbergen; off Halifax and on the Grand Banks it reaches a comparatively large size, while off the western coast of Greenland it attains a diameter of 500 mm. or more, reaching 700 mm. in the Okhotsk and Japan Seas.

The west coast of Greenland abounds in fjords which are continually giving off fresh water ice which floats away, melting as it goes, thereby killing millions of small organisms which are unable to endure a great change in the salinity of the medium they inhabit; these fall to the bottom and furnish an abundant supply of food for the

[1] Stimpson's *Alecto eschrichtii* from Grand Manan is in reality *Hathrometra tenella.*

crinoids there, which consequently are enabled to attain very considerable dimensions. In the Kara and Barents Seas there is no such supply of fresh water at hand, hence the crinoids are small, but Spitzbergen, through its snow fields, and the consequent freshening of the surface water about it, allows the crinoids along its shores to reach a larger size than those of the Barents and Kara Seas, though they are not nearly so large as are those from west Greenland.

Over the Grand Banks the Gulf Stream brushes by, and mixes more or less with, the cold northern current; this is fatal to the delicate southern life it contains, which is killed and precipitated to the crinoids below; they, therefore, in spite of their living on the extreme southern limit of the specific range, are as large as, or larger than, specimens from Spitzbergen.

The Kuro Shiwo, or Japanese current, sends off a branch through the Korean Straits which washes the eastern shore of the Japan Sea, and in its northern part, from the Straits of Tsugaru to the Straits of La Pérouse mingles with the very cold water from the Okhotsk Sea. The mixing is very gradual and extends over a considerable territory, and over all this area the crinoids are of gigantic size, bearing witness to their enormous food supply. Now this colony of *Heliometra glacialis* var. *maxima,* a purely arctic species, replaced on the Pacific side of Japan and the Kuril Islands by widely different forms, and finding no close relatives nearer than the Kara Sea, might be supposed in the course of the years which have elapsed since the Okhotsk Sea was part of the Arctic Ocean, to have become rather widely differentiated from the parent stock, and to have gradually reached a larger adult size from some other cause than the question of food supply; fortunately, however, we are able to make some observations bearing directly upon this point. In this area, Heliometra is found where the bottom temperature is very low, about freezing or less; but dovetailed into these cold areas are others where the

bottom temperature is 40° F. or above. These warmer areas are occupied by a fauna radically distinct from the arctic fauna of the cold areas, though the depth is about the same, and we find in them crinoids belonging to the purely Pacific genera Thaumatometra and Psathyrometra. It is gratifying to note that the representatives of both these genera are far larger here than anywhere else, the difference, in fact, being relatively greater than in the case of Heliometra. These three genera here live among entirely different surroundings, and in widely different temperatures; but their food supply, coming in a rain from above, is the same, and is, moreover, the only common ecological factor; therefore, there is no room for doubt that the food supply is the cause of the great increase in size.

While the recent pentacrinites as a rule live below 100 fathoms, in certain places, such as in some localities along the northern coasts of Cuba and Guadeloupe, and in Suruga Gulf and Sagami Bay, Japan, they approach much nearer the surface, and have even been taken in water of between 20 and 30 fathoms (Guadeloupe). Now Cuba and Guadeloupe are mountainous islands, while Suruga Gulf and Sagami Bay are close to that magnificent mountain Fuji-Yama, and to other high lands as well. The result is that many intermittent streams flow into the sea at these places, having their origin in the high lands; the rise in volume of their waters is so sudden that the pelagic life can not give way before it, but is killed and precipitated. The greatly increased food supply in the vicinity of one of these streams thus brings the food intensity up to such a level that the large pentacrinites may exist in such localities in much shallower water than would otherwise be possible. The water from these streams is never very great in amount, and does not penetrate deeply, but spreads out over the surface of the sea; thus a crinoid could exist very near the surface without being affected by it. Large rivers with a comparatively steady flow, on the other hand, freshen the

entire sea for a large distance from their mouths, and thus render crinoid life impossible.

Within the tropics, particularly in the East Indies, very large comatulids belonging to the Tropiometridæ, the Zygometridæ, the Himerometridæ, and the Comasteridæ occur abundantly in very shallow water, often just below the low tide mark; moreover, they decrease in size with depth. This would appear to directly contradict the conclusion reached in the case of *Antedon bifida,* but in reality the problem is an entirely different one. Within the tropics the intense scorching sunlight causes rapid evaporation from the surface of the sea, especially where the water is shallow, and a consequent mortality among the more delicate organisms. The beaches and rocky shores, at low tide, warm up, to be covered again at high tide with comparatively cool water, full of organisms unable to stand a great difference in temperature, which are consequently killed and swept back into the sea, to fall just beyond the low tide mark. Periods of glaring sunshine are relieved by torrential rains, which are just as fatal to pelagic life through the sudden lowering in the density of the surface water. Thus it is evident that within the tropics the sublittoral zone and the sea bottom near the shore line offer the maximum food supply for the crinoids, and explain the occurrence in such localities of members of these four families of very large size.

But torrential rains are associated with mountainous districts; a glance at the distribution of the species of these four families shows that all of the large species and practically all of the small ones occur exclusively about mountainous islands or near high mainland, and they are particularly abundant along the shores of the larger East Indian Islands. On isolated coral reefs and about the shores of low coral islands where, owing to the very low altitude of what little land there is the rainfall is very small, these large littoral crinoids are quite absent.

The comatulids are divided into two great groups, one with triangular pinnules and small eggs, the Thalas-

sometroida, the other with round pinnules and large eggs, the Antedonoida. The forms with small eggs, being no smaller than those with large eggs, may reasonably be supposed to require a longer period for development. This would imply a greater duration of the free swimming larval period, which would result in greater powers of dispersal, hence a greater geographic range. Moreover, a slowly developing larva might be supposed to possess a greater power of adaptation to environment, and therefore a certain ability to colonize new places under changed conditions, for instance, to spread downward to great depths.

The genus Thalassometra, genus of the Thalassometroida (with small eggs) has the widest distribution of any comatulid genus known, geographically and bathymetrically. It is found throughout the tropics, northward to the Aleutian Islands, the West Indies and Portugal, and southward to South Africa, the Crozet Islands and Australia; in depth it ranges from about 50 to 1,600 fathoms. Charitometra and Tropiometra, two other genera of the same group, are both intertropical, and the former reaches very considerable depths. The genera belonging to the Antedonoida (with large eggs) are mainly comparatively local and do not occupy large bathymetric altitudes. Though a number are littoral and one inhabits the greatest depths from which crinoids are now known, the bathymetric range of each is small, far smaller than that of the genera of Thalassometroida.

The beautiful and brilliant coloration of the crinoids has often been remarked; so striking is the common European species, *Antedon bifida*, that it has formed the subject of colored plates by Heusinger, Dujardin, Dalyell, Dujardin and Hupé, and Gosse; but the larger tropical species are much more varied and handsome (though colored figures of them have been published only by Leach, and by Kuhl and van Hasselt) and are, for the diversity of their markings and the delicacy of their hues

unrivaled among the marine invertebrates. Observers have contented themselves with making short color notes, each on a very limited number of species, and no one has as yet made this phase of the subject an object of study, yet there appear to be many interesting points well worthy of record.

All colors are found in the crinoids except blue, though true black is confined to the disks of the Pentametrocrinidæ and to lines and spots on two species of Coccometra, and may therefore be omitted from a general discussion. Both blue and black, however, enter largely into combinations.

Yellow is the commonest color in the group, and is the color of all the more primitive forms, and of the young of almost all the others; it may, therefore, be taken as the fundamental basic crinoid color. The pentacrinoids of *Antedon bifida* are sometimes pink, though usually, like the pentacrinoids of the other forms in which they are known, yellow, and certain other forms are dull pinkish at all stages. We may, therefore, assume two basic colors, yellow and red, the latter an intensification of the former, found generally in the more specialized forms.

The derivatives from these two basic colors as they occur in the crinoids may be grouped as follows:

I. Yellow	+ [Blue]	=	White. / Green.
	+ [Black]	=	Brown.
II. Red	+ [Blue]	=	Purple; maroon. / Violet.
	+ [Black]	=	Crimson.

Under the first heading come:

Yellow: Bathycrinus, Rhizocrinus, Ptilocrinus, Phrynocrinus, Nanometra, Adelometra, Trichometra, Heliometra, Atelecrinus, and all but very large specimens of the species of Thalassometridæ.

White: Asterometra; markings on shallow water Thalassometridæ.

Green: Hathrometra, Coccometra, Leptometra, Compsometra.

Brown: Very large specimens of all the species of Thalassometridæ, Thaumatometra, and Thysanometra.

Under the second heading come, Zenometra, Psathyrometra, Bathymetra, Isometra, the Pentametrocrinidæ and Hypalocrinus.

No species is known which exhibits a perfect blending of these two basic types or their derivatives, though there are many mosaics in which both are found side by side, either in different individuals, or, more usually, in the form of a color pattern, made up partly from one base and partly from the other (each being clearly defined) in the same individual.

Some mosaic species, such as *Tropiometra afra* and certain of the Comasteridæ are peculiar in that some specimens belong exclusively to type I (yellow) and others exclusively to type II (violet) but none are ever mixed.

The mosaics are, the Zygometridæ, the Comasteridæ, the Thopimetridæ except Asterometra, Iridometra, Antedon, Erythrometra, Perometra, Hypalometra, Promachocrinus, and the Himerometridæ.

The data seem to show that the smaller stalked forms are invariably and unchangeably yellow, which color may be, as in the case of the parrots among birds, equivalent to a lack of color. Black is added to the basic color of comatulids at all depths, and appears to denote age. Blue is added apparently only within 200 fathoms of the surface, and increases in intensity to the surface. The mosaics are all littoral or shallow water types.

Species growing among coral or on white bottoms in shallow water are very dark in color, often nearly black or sharply black and white, while the same species on mud may be light yellow and pinkish; or a species may be purple and yellow in comparatively deep water, and violet and white in shallow water. We seem to be able to trace a close connection between color and amount of illumination, the blue factor in the coloration increasing with the light.

There appears to be no direct relation between the color of crinoids and their environment. The yellow deep water species are very conspicuous in the mud from a deep dredge haul, while the color of shallow water species, as just indicated, is commonly in great contrast to their surroundings. Crinoids can have little to fear, because their extremely calcareous organization would seem to make them very undesirable as food; on the other hand, a strongly contrasting coloration might be of advantage in attracting small organisms, as contrast spots on flowers do insects; observations in this point would not be difficult to make, and might lead to interesting results.

The other echinoderm classes appear to be in general subject to the same laws of color change as the crinoids, but the records are much more complete and satisfactory, and the specimens are not so much changed in preservation. They would, therefore, offer an interesting field for study.

These are some of the more interesting inferences to be deduced from an examination of the literature on the Crinoidea in its present state; and, in view of the great geological importance of the group, and its bearing on important geologic problems, it is to be hoped that this phase of the subject, as well as the systematic and anatomical sides will in the future receive its due attention.

SHORTER ARTICLES AND CORRESPONDENCE

EVOLUTION WITHOUT ISOLATION

Is isolation a factor of evolution? The answer must depend, obviously, on what we mean by evolution, as well as upon the relations of the facts. Every difference of opinion regarding the nature and causes of evolution involves the use of the word in a different sense, unless the process is to be renamed with each change of interpretation. The choice of words is worthy of careful consideration, but words should not lead us away from the broader issue of biological facts. The practical question is not whether the words or their senses are new or unusual, but whether the facts are correctly represented.

Being convinced that changes in the characters of species are spontaneous, I apply the word evolution to these spontaneous processes of change. This, of course, is not the meaning of those who believe that changes in species are brought about by external influences working upon normally stationary groups, who have been accustomed to think of evolution as a passive result of change in the environment, rather than as an active process, inherent in the species.

From one point of view evolution appears as a complex of different kinds of environmental influences, from the other as a process of growth in the species, somewhat analogous to the development of individual organisms of which species are composed. In the one case the species are thought of as being carried or pushed along by their environments, in the other as advancing by motions of their own, often in spite of environmental obstacles and deflections.

Belief in isolation as a factor of evolution marks an intermediate stage of opinion between those who hold that natural selection causes evolution, and those who reject selection as a cause. The effort is to maintain the doctrine of environmental causes by giving selection the assistance of other alleged factors, such as isolation, mutation, environmental variation, heredity, ontogeny, etc. Nevertheless, this course has its logical dangers for the theory of selection, for the placing of much emphasis on isolation is practically equivalent to saying that evolutionary

changes go on of themselves, without the need of environmental interference.

If we advance with sufficient confidence in isolation we eventually come through to the realization that our alleged environmental factors are unnecessary as causes, because evolution is spontaneous. This approximation of views has been recognized by Dr. John T. Gulick who states in the January number of the AMERICAN NATURALIST that our interpretations differ only in the meaning attached to the word evolution.[1]

I am naturally very much pleased to agree with Dr. Gulick, for no other student of isolation has given the subject such extensive and thorough study. I subscribe to Dr. Gulick's statement that there does not seem to be any essential difference between us regarding facts. The difference is that the facts appear to me as of more significance than Dr. Gulick has represented. In attempting to point out this greater significance I have used a different method of expression.

To say that isolation and selection are factors of evolution should mean, in simpler English, that they cause evolution, or at least help it along, whereas they do neither. They appear to cause or to conduce to evolution only so long as we take it for granted that changes in the characters of species are dependent upon the subdivision of species, to form additional species.

The separation of a species into two or more parts allows the parts to become different, but there is every reason to believe that evolutionary changes of the same kind would take place if the species were not divided. That the isolated groups become different does not indicate that isolation assists in the process of change. It gives the contrary indication that changes are restricted by isolation. If isolation did not confine the new characters to the groups in which they arise, the groups would remain alike, instead of becoming different. Thus it appears to me that the danger of confusing the issues is much greater when we say that isolation and selection *are* factors of evolution, than when we say that they are *not* factors of evolution, however important they may be in multiplying and differentiating species.

Sufficiently narrow forms of isolation no doubt affect plants and animals in nature in the same way as the "intensive segre-

[1] Isolation and Selection in the Evolution of Species. The Need of Clear Definitions. *The American Naturalist*, 42: 48, January, 1908.

gation" by which domesticated types are induced to change some of their characters, but it does not appear that this intensive segregation is a condition of evolution. Differences between small groups are more obvious and more readily definable because small groups are generally more uniform, like the pieces with uniform patterns which may be cut from a variously figured fabric. Isolation is the shears that splits the species, not the loom that weaves it. The weaving is done when the fabric is broad. The larger and more diversified species make the truly constructive evolutionary progress.

The evolution of a species is in no way dependent upon its being split into smaller groups, but is more likely to be hindered by narrow subdivisions. If the groups are too small they degenerate and become extinct, instead of continuing their evolution. Isolation, though making more species, impedes evolution. In like manner, selection favors adaptation, because it keeps species from evolving in non-adaptive directions. Isolation and selection may still be considered as evolutionary factors if this time-honored reckoning is too sacred to be changed, but they must stand as negative factors instead of positive, if my interpretation is correct.

Darwin saw in his later years that evolution is not altogether the same as the formation of new species, and used in a letter (published after his death), the word "specification" as a means of expressing this distinction, a suggestion which I unwittingly repeated in proposing the slightly different word "speciation."[2]

> There are two different classes of cases, as it appears to me, viz., those in which a species become slowly modified in the same country (of which I can not doubt there are innumerable instances) and those cases in which a species splits into two or three or more new species, and in the latter case, I should think nearly perfect separation would greatly aid in their "specification," to coin a new word.[3]

Darwin was concerned to show that species multiply and diverge in nature, for this is good evidence of the general fact of evolution. Nevertheless, it should not be assumed that all forms of divergence represent evolution, or that divergence is a true measure of evolution. Divergence may be less than evolution, for the evolutionary paths of related groups often follow

[2] Factors of Species-Formation, *Science*, N. S., 23: 506.

[3] Life and Letters of Charles Darwin, 2: 339. New York, 1896.

nearly parallel directions. Divergence may be greater than evolution when changes are not progressive but sideways or backwards. Mutations, reversions, or degenerations, can take place suddenly, without the slow and gradual weaving of new characters in the network of descent of a species; they involve only the suppression of characters or the return to expression of old characters that continue to be transmitted in latent form.

As long as Dr. Gulick lets it appear that the divergencies of his snails arise through isolation, I fully agree with him, but not when he seems to suggest that isolation and selection produce new characters. The fact that isolated groups have no mutual sharing of evolutionary progress leaves them free to become more and more different, but the isolation does not explain the progressive changes to which the differences are due. Isolation explains *speciation,* but does not explain *evolution.*

This is the same objection that Darwin made to Wagner's theory of isolation, that it did not help him to understand "how or why it is that a long isolated form should almost always become slightly modified." Dr. Gulick explains that his interpretation differs essentially from that of Wagner, who held that even natural selection must have an "isolated colony" to work upon. Nevertheless, it appears that Darwin's objection applies to Gulick's doctrine as well as to Wagner's, for isolation only reveals the fact of evolution, while a genuine "factor" should do something toward explaining it.

Such a factor Darwin believed that he had found in natural selection, but he saw in isolation alone nothing to aid evolution. Darwin took it for granted that species were *normally stationary* and most of his successors still accept this unevolutionary assumption. With Darwin evolution was a definite process by which the characters of a species are changed, but with some of our later writers it has become merely a general name for a subject of study, whose various phases or branches are loosely called "factors," though they have no apparent relation to the original concrete idea of evolution as a process of change in species.

The failure to give a more definite recognition and a name (evolution or otherwise) to the processes of spontaneous, progressive change in species, appears to me to have prevented the attainment of the complete clearness sought by Dr. Gulick in the presentation of his elaborate and valuable evidence that only

isolation is needed for evolutionary divergence to become manifest. If Dr. Gulick really agrees with me that evolution is spontaneous, I must submit that his adherence to the custom of treating isolation and selection as factors has served to conceal his conclusions, rather than to announce and defend them.

O. F. COOK.

WASHINGTON, July 16, 1908.

A NOTE ON THE SILVERSIDE

In view of its value as a food fish, and as food for other more valuable fishes,[1] the following note on the habits of the silverside has special interest.

At Chesapeake Beach, Md., April 19, 1908, P. M., the tide was rising and probably pretty well up. At points where weed and such riff raff was partially buried in the beach, in the wash of the ripples which followed one another in, numerous fishes were wiggling actively as though stranded. At times one would be almost or quite clear of the water, but so active were they that the writer, not having a net, was at first unable to capture any. They evidently knew what they were doing, as when a spot they occupied was approached, they disappeared from it. Finally, by striking quickly with a piece of wood at a place where some were congregated, three were disabled and secured, which proved, as anticipated, to be *Menidia menidia.*

Examination of a specimen of beach trash collected where the fishes were observed, at the time, shows the presence of a number of eggs, apparently of *Minidia,* strong evidence that the fish were spawning. These eggs are one mm. or a little more in diameter and bear filaments at one point which attach them to the beach material in which they occur more or less scattered. The white color of the egg (preserved in alcohol) is relieved by yellow oil masses. This spawning ground, if such it was, would certainly be exposed at low tide. The species, in this case its northern race, has previously been noted to spawn above low-tide level.[2] Chesapeake Bay is neutral ground between the northern and southern races of *Menidia menidia,* and the writer prefers to refer the specimens obtained to neither race.

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[1] W. C. Kendall. U. S. Fish Comm. Rept., 1901 (1902), p. 241.

[2] H. C. Bumpus, *Science,* N. S., Vol. VIII, No. 207, p. 851, Dec. 16, 1898.

NOTES AND LITERATURE

BOTANY

The Origin of a Land Flora.[1]—Speculations concerning the origin of the higher plants have always had a special attraction for the botanical student whose work extends beyond the limits of mere collecting and tabulation. Perhaps the very fact that we can never expect to discover all of the factors concerned with the evolution of the vegetable kingdom, and that our conclusions are always liable to be materially altered through the discovery of new facts, or a different interpretation of those already known, gives an added zest to the hunt for new forms or the discovery of new facts about those already known which may add another stone to the edifice which is being slowly built up.

The volume under consideration is one deserving more than passing attention from the student of plant evolution. Not only is it the work of one of the keenest investigators of some of the most difficult problems with which the botanist has to deal, but the book represents the fruits of many years' arduous labor, but evidently a labor of love, which has yielded results of the utmost importance and provides a mine of accurate information, presented in an unusually clear and attractive style. From a literary standpoint, it might well be recommended as a model to some of our scientific writers who, it must be confessed, do not always compare very favorably with their English colleagues in the matter of literary form.

Aside from the wealth of facts brought together in this handsome volume, illustrated by many admirable illustrations, the reader constantly encounters speculations, sometimes almost startling in their originality, with which he may not always agree, but which are certain to set him thinking deeply; and we believe that this book will be a great stimulus to the further exploration of many obscure, but very important, questions bearing upon the affinities of the higher plants.

[1] The Origin of a Land Flora: A Theory based upon the Facts of Alternation. By F. O. Bower, ScD., F.R.S., Regius Professor of Botany in the University of Glasgow. Pp. xi + 727, many illustrations. New York, The Macmillan Co.; London, Macmillan and Co., Limited. $5.50 net.

It is not necessary to remind botanists of the high standing of Professor Bower's numerous contributions to science. Not only has such work as his great monographs on spore-producing organs put him in the first rank of morphologists, but his interpretation of the facts of comparative morphology, and his more speculative papers on alternation of generations and the origin of the land plants, have strongly influenced all recent theories on these important questions. Professor Bower is thus peculiarly fitted to treat this difficult subject, and it is with special gratitude to the author that botanists will welcome this admirable presentation of the results of his many years' labors.

It is generally admitted that the existing land flora, *i. e.*, the Archegoniatæ and seed plants, are the descendants of some fresh-water plants probably allied to certain green algæ; but the way in which these typically aquatic organisms gave rise to forms markedly terrestrial in habit is one of the questions about which there are very diverse opinions. Professor Bower has long contended, and we believe that he has overwhelming evidence on his side, that the characteristically terrestrial modern plant type, *i. e.*, the sporophyte or neutral generation of the ferns and seed plants, is the product of the evolution of the zygote or resting-spore of some fresh-water algal type, the result of the union of the sexual cells, or gametes, and in most cases is an adaptation to surviving periods of drought to which these plants are liable. That is, the sporophyte is from its inception a terrestrial or subaerial phase interpolated between the active aquatic growth periods. This is the "antithetic" theory of alternation, and it is this thesis, opposed to the "homologous" alternation which of late has been defended by a number of eminent botanists both at home and abroad, that Professor Bower defends in the present volume.

In his previous work, Professor Bower has elaborated his theory of the important part that the sterilization of potentially sporogenous tissue has played in the evolution of the sporophyte of the higher plants. Particularly has he made this clear in his important series of monographs on the development of the spore-producing organs of the Pteridophytes. The present volume is divided into three parts: (1) The Statement of the Working Hypothesis, (2) Detailed Statement of Facts, (3) Conclusion.

It has been rather the fashion of late to belittle the importance of comparative morphology, as it is evident that the plant organ-

ism, with its potentially unlimited power of regeneration and growth, is extremely plastic and responds promptly to any external stimuli. Nevertheless, the facts of comparative morphology are too evident to be ignored, and although the modern student must carefully check his work by the data furnished from experimental morphology, physiology, and paleontology, it still is evident that the surest clues to relationship must be sought in a comparison of corresponding structures and the facts of ontogeny.

The phenomena of alternation of generations as exhibited by the higher plants are familiar to the botanist. The plant shows two marked life phases, first the sexual phase, or gametophyte, and second the neutral generation, arising from fertilization, the sporophyte. In all but the highest plants, the seed plants, the gametophyte betrays more or less clearly its aquatic origin. It is usually poorly adapted to resist dryness. Water is necessary for fertilization, as the male gametes are ciliated and the mature sexual organs require water for their proper dehiscence. In the lower types, like the simple liverworts, the gametophyte is relatively larger and plays a much more important rôle in the plant life than does the insignificant sporophyte, which is short-lived and dies as soon as it has shed its spores, whose production is the aim of its existence. The sporophyte in the lower forms is never an aquatic structure, but receives its water indirectly from the gametophyte with which it is permanently in intimate association.

With the increasing specialization of the Archegoniates, several lines of development were inaugurated showing several different types of specialization both in the gametophyte and in the sporophyte. The gametophyte reaches its culmination in the higher mosses which seem to show the limit of the possibility of adapting the essentially aquatic gametophyte to life on land. The further development of the land plants is therefore bound up with the elaboration of the terrestrial phase of the plant's life history, *i. e.*, the sporophyte. With the increasing importance of the latter there is a progressive reduction of the gametophyte which culminates among the Pteridophytes in the extremely reduced gametophytes of the heterosporous forms like Marsilia or Selaginella.

It is not likely that any existing liverworts represent very nearly the direct ancestors of the Pteridophytes or "Vascular

Cryptogams." It may be said, however, that some remarkable parallelisms, if not real homologies, are shown by the peculiar Anthocerotes, and there is a progressive development of the sporophyte in both liverworts and true mosses which hints at least at the course of evolution which finally resulted in the entirely independent sporophyte of the ferns. The evolution of the sporophyte consists in a constantly increasing development of sterile or non-sporogenous tissues, which assume the character of green assimilative tissue, etc., and it may finally develop definite external organs, roots and leaves, the former connecting the sporophyte with the earth and making it quite independent of the gametophyte. Finally, spores are produced, always in a perfectly uniform manner in groups of four, and the life history is complete.

While only a relatively small number of forms have been investigated, it is pretty certain that the sporophytic tissues normally have nuclei with twice the chromosome number found in the cells of the gametophyte, this being the result of the doubling of the chromosomes due to the fusion of the gametes. The reduction of the chromosomes occurs in the tetrad division resulting in the spores, which therefore possess the normal gametophyte number.

The formation of the sporophyte by apogamy or direct budding from the prothallium, and the various buddings of the gametophyte from the leaves of the sporophyte, are the strongest arguments in favor of "homologous" alternation; but the facts of apogamy and apospory may be explained as cases of adventitious budding analogous to so many cases found in the seed plants, and much more evidence is needed to show that they are normal rather than pathological.

Comparing the sporophytes of the Bryophytes and Pteridophytes, the latter are distinguished by the development of external organs. A more or less conspicuous central axis has appendicular organs, leaves, roots and sporangia, the latter being the characteristic organs which distinguish the different types of vascular plants. They may be supposed to have arisen from the more or less complete segregation of masses of sporogenous tissue from the originally continuous layer of some such form as Anthoceros. The gradual evolution of the sporangium from the large indefinite sporocysts like those of Ophioglossum to the very definite sporangia of the highly

specialized leptosporangiate ferns can be clearly followed in existing types. Professor Bower does not regard the Ophioglossales as related to the true ferns, but from this view we feel obliged to dissent.

As might be expected, much stress is laid upon the "Theory of the strobilus" with which Bower's name is especially associated. This theory assumes that from some bryophytic sporangium, perhaps not very different from that of Anthoceros, by the segregation of definite sporangia each subtended by a leaf-like organ originating from the sterile tissue between the sporangia, a cone or strobilus would be derived, *i. e.*, an axis upon which are borne a number of leaves usually spirally arranged, each one subtending a sporangium. This condition is still met with in some of the simple species of Lycopodium like *L. selago* and it is an extremely ancient one.

This theory of the strobilus when applied to the Lycopods has very much in its favor, and is certainly the most plausible explanation yet put forward as to the origin of the Lycopods; but is not so convincing when one tries to reduce the ferns also to the strobiloid type. It is true that in the Cycads, which are doubtless of fern affinity, a strobilus is present, but there is very strong reason to suppose that it is a secondary condition.

The chapter on "Embryology and the Theory of Recapitulation" is a very sane treatment of an extremely difficult problem. While recognizing that the first students of vegetable morphology went much too far in their insistence upon the importance of the exact succession of cell divisions in the young embryo in their relation to the subsequent organs of the plant, nevertheless it is unquestionable that the early divisions of the embryo are to a certain extent a recapitulation of the early phylogeny. It must be remembered that the young embryo has been subjected for countless ages to practically the same conditions, and that under these conditions certain definite early segmentations should be fixed is merely what would be expected. One of these conditions is the action of gravity and this beyond question is the most important factor in determining the marked polarity of the embryo. As to the general application of the theory of recapitulation to the later stages of development, as Professor Bower very well points out, great caution has to be used, but nevertheless within proper limits it is justified.

Professor Bower maintains that there is but one type of leaf.

All leaves, he thinks, are primarily sporophylls. Foliage leaves are reduced sporophylls and cotyledons, and "protophylls" mere modifications of the foliage leaves. This is not, however, a view that can be accepted without some qualification. While undoubtedly on the theory of antithetic alternation, spore-bearing structures must have preceded foliage leaves, it may be questioned whether these primary spore-bearing structures at least in the case of the Ophioglossaceæ and Equisetaceæ, were not rather of the nature of sporangiophores than sporophylls in the strict sense of the word. If such is the case, the sterile leaves would be outgrowths of the sporangiophores, or even independent structures rather than direct metamorphoses of sporophylls.

From a study of the anatomical evidence, the conclusion is reached that the primitive state in the Pteridophytes was one in which the axis was structurally dominant in the shoot, and the type of cauline bundle a solid monostele. It is also concluded that the bipolar, radially symmetrical condition of the sporophyte is more ancient than the dosi-ventral condition.

The problem of the origin of the roots of the vascular plants by means of which the independence of the sphorophyte is finally secured is recognized as a very difficult one. In some Lycopods no root is formed in the embryo until after several leaves have been developed, and the name "protocorm" has been proposed for this early undifferentiated plant-body, the assumption being made that it represents an ancient condition antedating a plant-body with true leaves. Professor Bower, however, is inclined to doubt the accuracy of this hypothesis.

While recognizing the great value of the evidence of paleophytology, and the important contribution that the study of fossils has made to our knowledge of the evolutionary history of the Pteridophytes it is pointed out how very little light has been thrown by this science upon such fundamental questions as the origin of the bryophytic sporogonium or that of the leafy sporophyte.

In chapter nineteen are discussed the difficulties of determining whether amplification or reduction has been the more important factor in determining the course of evolution in certain cases. Chapter twenty contains a succinct summary of the Working Hypothesis and concludes Part I.

Over 400 pages of text with many admirable illustrations are devoted to Part II, "A Detailed Statement of Facts." This is

an excellent account of the sporophytic structures of the Archegoniates and would by itself form an important volume. As might be expected in a treatise on land plants, and from the author's previous works, the Pteridophytes are the principal subjects of study, only two chapters out of twenty being devoted to the Bryophytes. Space forbids even an outline of the great mass of facts brought together, not the least interesting and important being those derived from a study of the fossil forms which of late have attracted so much attention. Very little space is given to the study of the gametophyte, and while no doubt in the problem of the origin of a land-flora the sporophyte is much the more important factor, still we can not but feel that in some cases, a careful study of the gametophyte would have resulted in some different conclusions and would have served as a useful check. Thus all the recent work on the gametophyte of the Ophioglossaceæ emphasizes the strong similarity in the reproductive organs of these forms and those of the Marattiaceæ and makes more probable than ever a real relationship existing between these two orders of eusporangiate ferns.

There are recognized three phyla or main developmental series of Pteridophytes, the Lycopods, the "Sporangiophoric Pteridophytes" and the ferns, excluding from the latter the Ophioglossaceæ which Professor Bower thinks at present had best be treated as a fourth phylum, although he concludes that there is good evidence of a more or less evident affinity with the "Sporangiophoric Pteridophytes."

The isolated position of the Lycopods is recognized by Professor Bower, and there certainly is very strong reason, both from a study of the gametophyte and sporophyte, for assigning to this group an origin quite apart from that of the other Pteridophytes.

The most radical departure from the ordinarily accepted arrangement of the Pteridophytes is the establishment of the group of "Sporangiophoric Pteridophytes" which includes the Equisetales and the fossil Sphenophyllales with which latter group are included the anomalous Psilotales, which have usually been associated with the Lycopods, but whose isolated position has for some time been clearly recognized. To the sporangiophoric Pteridophytes Bower also thinks the Ophioglossales may be related. The sporangiophore is defined as a more or less elongated vascular stalk upon which sporangia are borne. The sporangiophores are considered to be organs *sui generis* not a

modification of either a foliar or cauline organ. The question is left open whether the sporangiophore is to be regarded as the elaboration of a single sporangium, like that of Lycopodium, but it seems to us that the origin of the sporangiophore as a compound structure from the beginning, is more in harmony with the facts of comparative anatomy.

The acceptance of this view will we believe help to solve some of the most puzzling questions as to the affinity of the primary pteridophytic stocks. While convinced of the real affinity between the Ophioglossaceæ and the true ferns, we have also more than once called attention to the marked resemblance between the gametophyte of Equisetum and that of the lower ferns; and it may be added that there are also correspondences in the embryo that are probably not without significance. If then we admit that the sporangiophoric Pteridophytes really represent a natural division of the Pteridophytes, it is quite conceivable that from some common ancestral form having a large green gametophyte like that of the lower ferns, two types of sporangiophoric sporophytes may have arisen, one developing the strobiloid group of sporangiophores, as in Equisetum, the other a single large sporangiophore like that of Ophioglossum. There is very good reason to suppose that the sporangiophore of the Ophioglossaceæ is not an appendage of the so-called sporophyll, but is a quite independent organ, the sterile lamina being rather an appendage of the sporangiophore than the reverse.

In spite of Professor Bower's argument we can not but feel that the resemblances between the Ophioglossaceæ and the true ferns are too numerous and exact to be explained on any other ground than that of a real affinity; but this does not lessen the importance of his explanation of their probable affinity with the Equisetales and Sphenophyllales.

The classification of the Filicales excluding Ophioglossaceæ is that already elaborated in his memoirs on spore-producing members. Three groups of the Filicales are recognized. One, Simplices, in which all of the sporangia of a sorus are formed simultaneously. Two, Gradatæ in which there is a definite success in time and space; and Three, the Mixtæ in which there is a succession in time but not in space. Six families are included in the first group. The Botryopterideæ (fossil), the Marattiaceæ, Osmundaceæ, Schizæaceæ (Marsiliaceæ)? Gleicheniaceæ and Matonineæ. The Gradatæ include five families. Lox-

somaceæ, Hymenophyllaceæ, most Dicksonieæ, Dennstædtiinæ, Cyatheaceæ (Salviniaceæ)? The remaining families often grouped together as Polypodiaceæ form the group of the Mixtæ.

The Botryopterideæ comprise some of the earliest known fossil Filicales. Their affinities, however, are somewhat obscure, and the group seems to have been a synthetic one. They show certain evidences of affinity with the Marattiaceæ also with the Osmundaceæ and Hymenophyllaceæ. It might also be suggested that a comparison of the sporangium might be made with Botrychium and perhaps Helminthostachys.

We must pass over with brief mention the very detailed account of the ferns which occupies over 150 pages of the text. The tendency in the evolution of the sporangium is very clearly from the larger eusporangiate type of the Marattiaceæ reaching its maximum in Kaulfussia, where nearly 8,000 spores occur in the single sporangium, to the numerous, small leptosporangiate sporangia of the Mixtæ where there may be only from 8 to 64 spores. It may be added that the sporangia of Ophioglossum represent a still more primitive type, both in their large size, their indefinite limits and very great number of spores.

The assumed relation of the different families of the Filicales is graphically shown in the diagram on page 653.

Part III is a summary covering some sixty pages. The most important conclusion may be briefly stated as follows: "*Certain Algæ suggest in their post-sexual phase how the initiation of a sporophyte may have occurred, but there is no sufficient reason to hold them as being in the actual line of descent of archegoniate forms.*" "*Both Mosses and Liverworts may with probability be held to be blind branches of descent,* which illustrate nevertheless phyletic progressions that illuminate the origin of sterile tissues from those potentially fertile, and the establishment of a self-nourishing system in the sporophyte." "*It may accordingly be concluded as probable that the prothallus of early Pteridophytes at large was a relatively massive green structure, with deeply sunk sexual organs.*"

The Lycopodiales stand by themselves in the simplicity of the sporangial arrangement and constitute a type of extreme antiquity, which has come down practically unaltered to the present day. Their comparative study may be conducted independently of other phyla: for there is no reason to think that they were derived from any other known vascular type. . . . *The condi-*

tion actually seen in the 'Selago' type may be held as truly primitive, and Lycopodium Selago, *with its imperfectly differentiated shoot, is in fact a near approach in a living species to the ideal primitive form which emerges from wide comparative study of the phylum as a whole."*

"The functionally identical parts designated sporangiophores and sporangia are cognate parts; it appears probable that the sporangiophore is itself a consequence of elaboration of a simpler type of spore-producing member, of which the sporangium of Lycopodium *is an example, while the trabeculæ in* Isoetes *and* Lepidostrobus Brownii *suggest a mode of origin of the septate state. If this were so, then the sporangiophore would have been distinct in its phyletic origin from the bract-leaves, which habitually subtend the spore-producing members, whether they be sporangia or sporangiophores."*

"The phyletic relationship of the Sphenophyllales and Equisetales has undoubtedly been a very close one; the distinguishing features are not to be found in the primary plan or construction of the shoot, so much as in the secondary modifications of number and relation of the appendages, and of their branching, together with changes in the originally protostelic structure of the axis. Such considerations support the conclusion that the Sporangiophoric Pteridophytes constitute a brush of naturally related phyletic lines."

The Ophioglossales are regarded as an ascending series of forms the *"spike illustrating various steps in the increasing complexity of a body of the nature of the sporangiophore."* "The whole unbranched shoot is a single strobilus bearing leaves of which all are potentially fertile and the majority actually so." *"The Ophioglossaceæ appear to have been an upgrade sequence, sprung from some sporangiophore stock, and bearing no near relation to the large-leaved ferns."*

"The Filicales were ultimately of strobiloid origin, but have undergone amplification of their leaves analogous to, but phyletically quite distinct from what is seen in other Pteridophytes, and carried to a higher degree."

"One chief reason for regarding the lines of the Filicales and Ophioglossales as distinct lies in the difference of position of the spore-producing members. It has been argued above (p. 633) that the soral condition was primitive for ferns, and that *the sorus is a body similar in kind to the sporangiophore, the two*

being alike in function, in structure, and in capacity for fission and extension: the number and position are points of difference."

The Filicales are considered to be a phylum showing fundamentally the strobiloid characters, but secondarily modified in relation to their pronounced megaphyllous habit. "*Accordingly, the Filicales appear as the most divergent phylum of homosporous Pteridophytes.*"

"*Comparison of the several phyla, as represented both by their fossil and their modern representatives, leads in each case towards the recognition of a primitive type, and its construction in the several phyla has certain features in common.* The chief of these are the definition of axial polarity in the first initiation of the embryo: the continued apical growth; the radial construction of the shoot: the origin of the appendages laterally from the axis by enation, and in strictly acropetal order: a protostelic structure of the conducting system of the axis, and a leaf-trace composed of a single strand."

"The sporophyte . . . probably arose originally as a structure of limited size, and unbranched, upon a prothallus of considerable dimensions, and producing *Homosporous Spores.*"

"The adoption of *Heterospory*, and of the *Seed Habit* supervened later. This, while it has led to the final independence of the land flora as regards external fluid water for the completion of its life-cycle, has brought as a secondary consequence a widespread reduction."

"The final goal of all organic development is the establishment of new individuals. The evolutionary story of the sporophyte illustrates this in two distinct ways. *In the prior and non-specialized homosporous forms large numbers of germs are produced: . . . consequently amplification of the whole sporophyte is the leading characteristic of these earlier types; . . . In the later and more specialized heterosporous forms and particularly in the Seed Plants with their more refined methods, individual precision supersedes mere numbers; and reduction of the propagative system has been its usual concomitant.*"

"The sporophyte, which is the essential feature in the Flora of the Land, is referable back in its origin to post-sexual complications: *it appears to have originated as a phase interpolated between the events of chromosome-doubling and chromosome-reduction in the primitive life-cycle of plants of aquatic habit.*"

DOUGLAS HOUGHTON CAMPBELL.

PLANT CYTOLOGY

Apogamy in the Ferns.—It has long been known that the archegonia in a number of ferns are not functional and that in these forms the sporophyte generations arise as vegetative outgrowths from the gametophytes. This suppression of sexuality with the development of the succeeding generation asexually is termed apogamy. Only recently, however, have there been any cytological investigations of the phenomenon.

Farmer and Digby[1] were the first to study the nuclear behavior throughout critical phases in the life history of apogamous ferns. The results, based on forms of Lastrea, Athyrium, and Scolopendrium, led these authors to describe three conditions.

1. The process of sporogenesis is omitted from the life cycle in three varieties of *Athyrium Filix-fœmina* and in a form of Scolopendrium giving the condition of apospory known for a number of ferns. The prothallia arise directly from abortive sporangia or from pinnæ; the sporophytes develop apogamously from the prothallia or from unfertilized eggs; and the approximate number of chromosomes is retained throughout the life cycle. This type of life history brings apogamy into close association with apospory. The omission of the process of chromosome reduction, characteristic of sporogenesis, gives the gametophytes the sporophytic number of chromosomes (2x). Apogamy seems to be a natural consequence, for gametes would not be expected to function under such conditions since they would double the number of chromosomes with each nuclear fusion and there would be no reduction divisions to bring the higher numbers back to the normal. These conditions in the ferns agree with certain cases of apogamy among the seed plants (*Antennaria alpina, Thalictrum purpurascens,* and apogamous species of Alchemilla and Hieracium) where the reduction mitoses are omitted in the ovule and the nuclei of the embryo sacs contain the sporophyte number of chromosomes, the embryo developing from unfertilized eggs or even from synergids. The most interesting feature of this type of life history is the development of gametophytes with the 2x or sporophytic number of chromosomes, showing that the morphology of this phase in

[1] Farmer, J. B., and Digby, L. Studies in Apospory and Apogamy in Ferns. *Ann. of Bot.,* XXI, p. 161, 1907.

the life history does not depend upon its containing the reduced number.

2. In *Lastrea pseudo-mas* var. *cristata apospora* apogamy and apospory follow one another in the same manner as described above, but the number of chromosomes (probably 60) is so close to that of the gametophyte in the type species (72) that it seems probable that in this form the sporophyte retains the reduced number (x) of the gametophyte. This condition is exactly the reverse of that noted above showing that the morphology of the sporophyte likewise does not depend upon its containing the double number (2x) of chromosomes.

3. The third and most striking conditions described by Farmer and Digby refer to a peculiar migration and fusion of nuclei in the cells of the prothallium just before the apogamous development of the sporophytes. These observations are recorded from the study of two *polydactyla* varieties of *Lastrea pseudo-mas* which form their spores with chromosome reduction in the usual manner. The nuclear migrations and fusions occur in the younger regions of the prothallia, in the wings as well as in the thicker portions. A nucleus assumes an elongated form with the pointed end against the wall which it is about to pierce. A pore is formed through which the nucleus slips and makes its way to the nucleus of this receptive cell which usually remains rounded. The two nuclei come to lie closely pressed against one another and gradually fuse. Older prothallia thus have fusion nuclei with double the gametophytic number of chromosomes (2x) and the cells of the apogamously produced sporophytes are found to have nuclei of this type; the authors conclude that they are derived from such fusion nuclei. This process of migration and nuclear fusion, taking the place of the fusion of gametes, finds its analogy in the recent studies of Blackman and Christman on the rusts. Just previous to the development of the æcidia there is an extensive migration of nuclei between neighboring cells so that the cells which give rise to the chains of æcidiospores contain conjugate or paired nuclei, the descendants of which remain in pairs until the nuclear fusion in the teleutospores. Thus in the rusts and in these ferns a process of nuclear fusion concerned with vegetative cells has apparently become substituted for the fusion of gametes which are no longer functional.

The most recent cytological contribution to the study of apogamy in the ferns is by Yamanouchi.[2] This paper gives a much more detailed account of nuclear structure and the behavior of chromosomes than that of Farmer and Digby, and is remarkable for the thoroughness of the study of critical phases throughout the entire life history. We have already noticed a portion of the work in the review of some recent research on cilia-forming organs of plant cells in the August number of the NATURALIST. Yamanouchi worked upon *Nephrodium molle* which has the advantage of presenting under ordinary conditions of culture the normal life history of ferns. The apogamous development of sporophytes may, however, be readily induced in prothallia exposed to direct sunlight and watered from below so as to prevent the possible escape of sperms and fertilization of archegonia. Such prothallia develop much more slowly than under normal conditions. After six weeks the cushion regions become markedly thickened, which thickenings indicate the beginnings of apogamous sporophytes.

Yamanouchi made very accurate counts of the chromosomes throughout the critical phases of the normal life history preliminary to a comparison with apogamous conditions. The chromosome number in the sporophyte is 128 or 132, which is reduced during sporogenesis to 64 or 66 in the usual manner. The gametophyte has then 64 or 66 chromosomes which were counted in the vegetative cells of the prothallia and in the mitoses leading up to the formation of sperms and eggs. The fertilized egg has of course the double or sporophytic number.

Prothallia, which under the culture conditions described above produce sporophytes apogamously, have 64 or 66 chromosomes. The mitoses up to the 30–50 cell stages are similar to those in normal prothallia. After that the growth is very slow and there are irregularities in the position of the cell walls with reference to the surface of the prothallia. The apogamous prothallia produce antheridia in abundance which develop motile sperms, the mitoses showing 64 or 66 chromosomes. Archegonia are, however, rarely formed on apogamous prothallia. Occasionally archegonia initials are differentiated, from which a central cell is cut off as in normal prothallia, but this central cell either remains undivided or produces eggs and canal

[2] Yamanouchi, S. Apogamy in Nephrodium. *Bot. Gaz.*, XLV, p. 289, 1908.

cells in an archegonium with a poorly developed neck; it is doubtful whether such eggs are capable of being fertilized.

The sporophytic outgrowths on apogamous prothallia arise coincident with the development of the cushion region. Superficial cells on the underside increase in size, and from one of these an apical cell is cut off which becomes the growing point of a leaf. Meanwhile there is a rapid division of the neighboring cells in the interior so that an area of meristematic tissue results which gives rise to the young sporophyte in direct connection with the prothallial cells. A leaf and stem axis are developed from two superficial apical cells, the root tip arises endogenously, scalariform vessels appear in the tissue connecting the developing leaf and stem, and finally there is differentiated the young sporophyte with root, stem and leaf regions. Mitoses are easily found in stages of this apogamously developed sporophyte and always show 64 or 66 chromosomes, the gametophytic number of the prothallium. Consequently, in *Nephrodium molle*, there is no doubling of the number of chomosomes in the development of apogamous sporophytes through nuclear migration and fusion as described by Farmer and Digby for the *polydactyla* varieties of *Lastrea pseudo-mas*. It has not yet been determined whether these apogamous sporophytes develop spores.

Apogamy in Nephrodium, therefore, presents conditions different from anything as yet recorded for plants, since following normal sporogenesis a sporophyte is developed with the gametophytic or haploid number of chromosomes (x), and there is no place in the life history for the diploid or sporophytic number. The case of *Lastrea pseudo-mas* var. *cristata apospora* is apparently not the same since in that form apogamy follows apospory. However it is possible that the apogamous sporophytes of Nephrodium may be found at maturity to develop apospory and thus swing into a type of life history similar to that recorded by Farmer and Digby for the above form of Lastrea. The most significant results of Yamanouchi's investigation is the clear evidence that the morphology of the sporophyte does not demand that its cells contain nuclei with the double or diploid number of chromosomes (2x), in other words that the "number of chromosomes is not the only factor which determines the characters of the sporophyte and gametophyte," a conclusion indicated by the known cases in both ferns and seed plants

where gametophytes have the sporophytic number of chromosomes.

A third paper which should be mentioned in connection with these two on types of homosporous ferns is Strasburger's[3] study of apospory in heterosporous Marsilia. Parthenogenesis had been reported by Shaw as occurring in 50 per cent. of the female gametophytes of *Marsilia Drummondii*. Nathansohn had induced parthenogenesis in *Marsilia vestita* and *M. macra* by keeping germinating megaspores at a temperature of 35° C. for 24 hours and then allowing them to continue their development at a temperature of 27° C. Under this treatment the eggs of 7–12 per cent. of the spores gave rise to embryos parthenogenetically while at lower temperatures embryos were only developed after fertilization.

Strasburger found that in *Marsilia Drummondii* the nuclei of the female gametophyte contain 32 chromosomes which is the sporophytic or diploid number present in various vegetative regions of the sporophyte. The process of sporogenesis presents various irregularities: the number of megaspore mother-cells is less than 16 and at times only 4; sometimes the mitoses within these cells are reduction divisions of the usual type (heterotypic), but in other cases spores are formed only through vegetative mitoses in which the sporophytic or diploid number of chromosomes (32) is retained. Such spores give rise to female prothallia with eggs having the sporophytic number of chromosomes and a parthenogenetic development of the latter follows. These conditions differ from those of apospory in the fact that spores are developed, but agree in the final result that the process of chromosome reduction is suppressed in the life history. The microspores showed irregularities in their development and on germination did not produce mature sperms. Two other species in the genus, *Marsillia macra* and *M. Nardu*, presented similar conditions.

Perhaps the most important feature of this cytological research on apogamy is its bearing on current theories of the nature and basis of alternation of generations in plants. It is perhaps rather generally held by those who accept the antithetic theory that the differences between sporophyte and gametophyte are in some way concerned with the number of chromo-

[3] Strasburger, E. Apogamie bei Marsilia. Flora, XCVII, p. 123, 1907.

somes, the sporophyte taking its peculiarities because of the doubling of the number which results from the sexual fusion of gamete nuclei, and giving up these characteristics when the number of chromosomes are reduced at the end of the sporophytic phase. This view that nuclear structure and more particularly the number of chromosomes gives the physical basis for alternation of generations was originally stated by Strasburger and has received support from a large amount of research on life histories throughout the plant kingdom. It has in the opinion of some authors reached the stage worthy of statement as a law of development, as indicated by the expression x and 2x generations applied to gametophytes and sporophytes.

However, the cytological investigation of apogamy in the seed plants as well as in the ferns has shown for a considerable number and wide range of forms that the gametophyte generation may have the sporophytic number of chromosomes, and now in Nephrodium there is established the first instance in which a sporophytic generation may develop with the gametophytic number.

This evidence may be regarded by some as cutting at the roots of the antithetic theory of alternation of generations, but this does not follow. It is clear that an increase or decrease in the number of chromosomes within a certain range does not affect the morphology of the phase of the plant's life history concerned, and the cause of the specific characters of gametophyte and sporophyte must rest upon other factors. What these may be is problematical; it is not unlikely that a variety of factors is concerned. It is probable that the peculiarities of every species demand at least a certain amount of chromatin with a specific composition, but there is no reason to assume that this must be contained in a fixed number of chromosomes, and furthermore multiples of the minimum amount required would not be expected to introduce new characteristics except as it might give increased vigor or vitality. Then there is the cytoplasm to be considered and perhaps of even greater importance the complex reciprocal relations that must exist between the nucleus and cytoplasm.

BRADLEY M. DAVIS.

EXPERIMENTAL EVOLUTION

Regeneration in Lumbriculus.[1]—In the August number of Roux's *Archiv* a paper by Conrad Müller describes regeneration in *Lumbriculus variegatus* and *Tubifex rivulorum*. The paper of 70 pages contains 24 figures and 14 full-page tables. Despite its bulk one can not help being impressed with its failure to contribute much that is new to our present knowledge of regeneration in Lumbriculus.

Müller's chief concern seems to be the extent of the power of regeneration. He first studied the power to regenerate a head or a tail in Lumbriculus, and from a great many experiments, very elaborately described, he found that new heads may regenerate 17–22 times in succession, while new tails regenerate 33–42 times after successive operations. From these facts he draws the general conclusion that the power of posterior regeneration is twice as great as the power of anterior regeneration. Bonnet in 1741, in his classical investigation of the regeneration in Lumbriculus, found also that heads and tails regenerate several times after successive operations—only Bonnet never obtained regeneration so many times.

These results of Müller may be, however, interpreted otherwise than that the power of posterior regeneration is greater than the power of anterior regeneration, since the worms regenerating tails had heads and could therefore feed, while the worms regenerating heads could not feed.

Regarding the relation between length of time during which a tail regenerates and the number of segments that are produced Müller sets up the following "law"—"The number of segments newly formed stands in direct relation to the length of time of regeneration; i. e., during equal periods of time there are regenerated posteriorly equal numbers of segments." He also investigated the number of posterior segments that regenerate after successive operations performed at regular intervals. In the course of ten months he cut off the regenerating tails 22 times (every 14 days) and found that in this case also "after repeated removals of a regenerating tail the same number of new segments is formed during similar periods of time." He then refers to my work on regeneration in Lumbriculus and says that, "Bei dem von Morgulis und mir behandelten Object scheint

[1] *Arch. f. Entwicklungs u. d. Organismen*, XXVI, 1908.

dass kein Unterscheid zu machen." But this "agreement" is due apparently to a misunderstanding. On the contrary, I got the opposite result in my studies on regeneration in Lumbriculus. I found that the number of segments formed within equal lengths of time decreases the more the time that has elapsed since the operation was performed. Concerning the rate of regeneration for similar periods of time (but after successive operations) my statement is so simple that it is surprising that it should have been misinterpreted. I said—" . . . in the course of the second period of two weeks the pieces regenerate about one half as many segments as when regenerating for the first period of two weeks." After a third period of two weeks "the pieces have regenerated only about one half as many segments regenerated for the second period of two weeks, and about one fourth as many as for the first two weeks."[2]

Müller quotes my general conclusion, based upon these facts, that "a piece of worm, when subjected to the operation of cutting a few times will produce more new tissue for the same length of time than when subjected to cutting only once," and says: "Desartiges habe ich ebenfalls beobachted."! But unless I misunderstood Müller's point, his "law" is the reverse of my conclusion. He says that a worm regenerates on an average 25 segments in 14 days; after the following 14 days it will have regenerated 50 segments, or 25 segments more, etc., so that the number of regenerating segments is in direct proportion to the length of time. His tables show also that when the tails have been cut off every 14 days 25 new segments regenerate each time. In other words, a worm left to regenerate for 8 weeks should regenerate 100 segments (25 segments every 2 weeks), while another worm in which the tail is removed at the end of every 14 days regenerates 25 segments after each successive operation, and, therefore, will also have formed 100 segments at the close of 8 weeks.

So that a worm that had been operated upon 4 times regenerates 100 segments in the same time in which another worm, that had been operated upon only once, also regenerates 100 segments. This certainly does not uphold my contention; it is also evident that Müller's "law" is incompatible with my conclusion cited above, yet he seems to find them both to be true. Müller speaks at great length of the regeneration of pieces of

[2] *Jour. Exp. Zool.*, IV, 1907, pp. 561 and 562.

Lumbriculus without adding anything new. His discovery that single segments are capable of anterior as well as posterior regeneration is not new, since I have shown in my paper, published ten months earlier, that single segments regenerate in this way. Although Müller reviews my experiments with single segments in full detail, he feels dubious as to whether I really did have single segments regenerating. The scepticism is due to the fact that, according to my description, the worms have been regenerating in clean water, and in Müller's experience "war das Halten der Tiere in reinem Wasser einfach ausgeschlossen." I may therefore mention in this place that pieces of Lumbriculus have been reared in clean water even by Bonnet, and that for the three years that I have been studying regeneration in Lumbriculus the worms were and are now *invariably* kept in clean water.

In the chapter dealing with the regeneration of regenerated pieces Müller makes no mention of my experiments, which in fact were the first experiments of that nature in Lumbriculus. He states that he got the regenerated tail, when detached from the parent body, to regenerate new heads or tails 23 times.

The fact that Lumbriculus can regenerate its head 23 times and its tail 42 times in succession is of considerable theoretical importance, and even more so is the statement that regenerated pieces are also capable of regenerating heads and tails many times in succession. It seems to me that these facts bear directly on the hypothesis of formative substances. If such substances are connected with the regeneration of a head or a tail it would be hard to conceive how such an enormous quantity of head- and tail-forming substances has become stored up in the cells to insure the possibility of regeneration after 23–42 operations, unless a further assumption is made that those substances themselves are capable of reproduction. Still harder would it be to conceive how a regenerated tail, the supposed product of tail-forming substances, has become stored up with such an abundance of reserve formative substances as to be able to produce heads or tails time after time. To make such a demand on our credulity would be asking a great deal.

Müller's work on Tubifex is practically a repetition of his work on Lumbriculus. There he finds that a head regenerates only when 4–6 anterior segments are removed, and does not regenerate more than 7 times in succession, while a tail may regen-

erate even 40 times. The successive regeneration of heads may be checked by the regeneration of the tail. Regenerated parts when detached from the worm are not capable of new regeneration.

The most novel part of the paper is that which describes various cases of heteromorphosis, and other malformations in the regenerating tail, including the regeneration of double tails in Lumbriculus or of triple tails in Tubifex.

SERGIUS MORGULIS.

September 7, 1908.

THE BUDGETT MEMORIAL VOLUME

John Samuel Budgett, naturalist, explorer, scholar and artist, was born in Bristol, England, in 1872. He received his education at University College in Bristol, and later at the University of Cambridge, where he received the appointment as Balfour Student in Natural Sciences, "the zoological blue ribbon of Cambridge." Here he gave, in 1902, a course of lectures on on the "Geographical Distribution of Animals," succeeding in this work the eminent ornithologist, Professor Alfred Newton. His work at Cambridge was interrupted and enriched by zoological exploring expeditions to South America and to Africa, efforts which from the natural history side were successful in the highest degree, but which ultimately cost him his life.

The first of these, in 1896, was to the Swamps of La Plata River at Gran Chaco in Paraguay, in search of the singular mud-fish, *Lepidosiren paradoxa*. The life history and embryology of this fish was expected to throw much light on the nature of the order of Dipnoans to which it belongs. All stages of the life history of *Lepidosiren* were represented in the collection made by Mr. Budgett, and the expedition was brilliantly successful.

On the next expedition, in 1899, he visited the Gambia River, where another genus, Protopterus, of the same group of mudfishes is found.

In the third expedition, in 1900, he visited the Gambia again, gathering material for not only the life history of the dipnoan, Protopterus, but of different species of the equally interesting

[1] The work of John Samuel Budgett, Balfour Student at the University of Cambridge, edited by J. Graham Kerr, University Press, Cambridge, G. P. Putnam Sons, New York, p. 422 quarto, with many engravings in stone. Price $7.00.

crossopterygian, Polypterus as well. With this was obtained material for the study of Gymnarchus and other peculiar fishes of the African streams.

In 1902, Mr. Budgett undertook an expedition to Nyanza and the head streams of the Nile.

A final trip was made in 1903, to the Niger River, in which, as in the others, he found species of Polypterus, and with which he made most interesting experiments in artificial fertilization.

In all of these expeditions, Mr. Budget found what he sought, and their importance to science can hardly be too highly estimated. The embryology, taxonomy and geographical distribution of these fishes, as well as of different genera of frogs, received notable accessions. But Mr. Budgett's health was sacrificed in the work. A recurrent attack of "blackwater fever," one of the many diseases known as malaria, caused his death on January 19, 1903, at the age of thirty-one.

The publications of Mr. Budgett give the record of these expeditions, and also discussions of the anatomy, the embryology and the breeding habits of Polyterus, Protopterus and other species. The batrachians of the Paraguayan Chaco are described in detail, and there is a paper on the birds of the Gambia River.

All these papers of Budgett, with others by Dr. G. A. Boulenger, Dr. J. Graham Kerr, J. Herbert Budgett, Richard Assheton, Edward J. Bles and Edward T. Browne, based on material collected by Mr. Budgett, have been sumptuously printed in the present memorial volume by Mr. Budgett's friends and fellow-workers at Cambridge. A delicately appreciative biographical sketch of Mr. Budgett is contributed by Dr. Arthur E. Shipley. In this are extracts from Mr. Budgett's diaries, showing his fine appreciation of nature and his charming and forceful use of English. The plates illustrating this volume are worthy of the text, and the whole is a noble memorial to an able naturalist, a brave and lovable man, who fell untimely from the hazards of his chosen calling.

DAVID STARR JORDAN.

ANIMAL BEHAVIOR

Mind in Animals.—Many experimentalists have said in their haste that all comparative psychologists are liars; that comparative psychology has no existence. To the experimental student of animal behavior, working by the methods of physiology and zoology, "psychic factors" are merely an irritating x, something which he can not perceive in his work, yet which the philistine is continually trying to force upon him as the cause of what he does perceive. Finding objective determining factors for all the objective phenomena, he has no use for the psychic factors, and finally decides to make war upon the whole worthless mess; Down with comparative psychology! is his cry.

But it is really only as a technician, intent on the proper methods for his own work, that the experimentalist can object to comparative psychology. As soon as he takes a wider view, he must perceive that another group of men have made a life specialty of precisely the matters that he leaves out of account, and he can not expect these men to give up their interest in the distribution and development of the phenomena that they are studying—of mind and mental processes. And so we have here two recent scientific works dealing with the presence of mind in animals, both from the experimental standpoint, one by a psychologist,[1] the other by a zoologist.[2]

Miss Washburn's book is of the greatest interest and value, supplying a need much felt. It will be the standard work for those who wish to know the present position of scientific animal psychology. Concerning the behavior of animals a large body of verifiable facts, which have begun to shape themselves into a more or less intelligible system, has been gathered together by experimentalists, but the latter have given little but hostile attention to the psychic aspects of the matter. What are the implications of this body of facts concerning the distribution of psychic processes among animals? This is the problem which Miss Washburn sets herself—a problem in which doubtless full as many are interested as in behavior as a purely objective

[1] Washburn, Margaret F. The Animal Mind: A Text-book of Comparative Psychology. New York, The Macmillan Co., 1908. $1.60. (Volume 2 of the Animal Behavior Series, edited by R. M. Yerkes.)

[2] Strassen, Otto Zur. Die neuere Tierpsychologie. Vortrag in der zweiten allgemeinen Sitzung der 79. Versammlung deutscher Naturforscher und Aerzte zu Dresden (1907). Leipzig und Berlin, B. G. Teubner, 1908.

science. One need not hold that psychic factors are required for explanation of the objective facts in order to see the great interest of this inquiry.

The author therefore examines systematically the behavior of animals, as discovered by experiment, from Amœba to the apes, attempting to show what psychic processes are, or may be, implied. She readily admits the possibility that no psychic processes are present at all; but the question is this: If we assume that psychic processes *are* present, and that they follow rules like those which they follow in man, then what ones appear to be present in the different groups of animals? In answering this question, the principle of parsimony is taken as a guide: "in no case may we interpret an action as the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale." The undeniable dangers of this, in the evident fact that nature doesn't always operate by what seems to our limited view the simplest means, is expressly recognized, but the principle is thought valuable for holding in check the common tendency to attribute higher intellectual faculties to animals—a tendency, we may remark, which in very recent times shows some inclination to change into its opposite.

After judicious introductory chapters on Difficulties and Methods; on the Evidences of Mind, and on Mind in the Simplest Animals, the main divisions of the book are devoted to Sensory Discrimination; Spatially Determined Reactions; Modification by Experience; the Memory Idea, and Attention. The devotee of popular animal psychology will be surprised to find that the word *reason* does not even occur in the index. The facts of behavior are set forth clearly and accurately; the student even of the strictly objective aspects of the subject will find this perhaps the best compendium of the important facts that exists. The treatment is throughout sane and conservative; it is analytic, systematic and scientific—not in any sense popular, though clear. Slips as to facts and details appear to be rare. All together the treatment appears to one not a psychologist—to one who "wants to be shown"—most satisfactory. Such a discussion of these matters by a competent psychologist has been much needed.

The book gives the experimentalist an opportunity to compare as to solidity and general satisfactoriness, his own objective

science, built up by systematizing the verifiable facts alone, with that which searches for the psychic processes underneath what is observed. The difficulties of making a positive science from the unverifiable psychic implications of the actions of animals is well illustrated by the conditional and potential forms in which the author is forced throughout to clothe her statements. Thus, in discussing the psychic aspect of orientation to light (p. 184), the predicates of six successive sentences are: we "cannot imagine"; we "may conjecture"; "is the human experience most closely resembling"; "appears to be"; "may have"; it "is possible that." The experimentalist becomes convinced more than ever of the need of building up his own positive science of behavior, composed of verifiable propositions, and omitting psychic factors—though there is no reason why he should look with an unfriendly eye on the attempt, as a separate thing, to supply conjecturally the missing psychic elements.

The difficulties in preparing a satisfactory account of the animal mind are further increased by the high degree in which the experimental science of behavior shares the provisional and uncompleted character of all science. Animal behavior even as a purely objective science is merely in its beginning. No greater mistake could be made (and this our author evidently recognizes) than to suppose that our present experimental knowledge is sufficient for defining sharply the psychic powers of animals. It is quite possible that the picture of the mind of one of the higher animals that might be drawn by an observing and judicious dog lover would be much more adequate than the rude sketch which experimental science is now able to give us. The material furnished by the old Anecdotal School, and by the Lovers of Nature, doubtless contains much most-important truth, to which the experimental method has not yet succeeded in attaining: only, as Miss Washburn says, it is not possible to tell what *is* true, what false. This material furnishes valuable finger posts for experimental investigation, but if we are ever to be able to distinguish the true from the false in animal behavior, it is necessary to build up the science by that slow and painful addition of one verifiable fact to another, which has proved the method of advance for other sciences. At any given time then our experimental science and the psychology based upon it are bound to be incomplete and inadequate to the reality. A single illustration must suffice. Miss Washburn shows that a careful

analysis of the experimental facts indicate that in Crustacea there is no color vision. But in the short period since her account was written, Minkiewicz has demonstrated experimentally a refined color vision in this group, the animals standing with much success the test of "matching colors" for their disguises. If in so comparatively simple a matter the negative indications were wrong, how much dependence can be placed on our now having a complete knowledge of what exists in higher spheres? Every experimenter knows how near he came to missing some important result that he finally reached; he realizes that there are doubtless many things equally important that he *did* miss. The positive results of experimental science are stones for building; the negative ones are often merely space as yet unfilled. Yet such summaries as Miss Washburn gives us of the knowledge at any particular time are necessary and valuable, especially when, as in the present case, they are put together by one fully conscious of the limitations of the subject.

Zur Strassen[3] in his lecture before the German Congress of Naturalists and Physicians deals with another aspect of mind in animals; with a question of the greatest practical interest to experimentalists, and of great theoretical interest to all. Are "psychic factors" required for explaining the behavior of animals, or can we explain the behavior throughout from the experimentally perceivable, objective, factors; can animals be understood as physico-chemical machines? Zur Strassen follows a course of reasoning which is often begun, but which usually stops in the middle; the author carries it to the end, with illuminating results.

As his guide he takes the principle of parsimony in its widest sense—that we shall not assume the existence of any factor which is not required in order to explain the results. A further principle, acted upon but not set forth in words, is that mere increase of complication, no matter how great, does not in itself imply a new principle of action. Under these principles he examines a series of examples of animal behavior in successive stages of complications, from Amœba to apes, concluding in each case that the entire behavior can be understood from the standpoint of physico-chemical causality, and that therefore we are not entitled to assume the presence of any psychic factor in the matter. The author is not inclined to add or subtract from

[3] *Loc. cit.*

the facts in order to maintain his thesis; he recognizes fully the complication of the behavior of both higher and lower animals; and he does not claim that we now know the precise physico-chemical factors involved in all behavior. But he is able to make a good case for his view that all is fundamentally intelligible physico-chemically; in other words, that we could ultimately make a complete and systematic explanation of what animals do, even if we assumed that they have no "psychic factors," no consciousness, at all. The nature of the objective explanations which to the author seem satisfactory he can of course merely sketch; there is no attempt to give details or claim finality. Most significant appears to him, as to others who have studied the matter, the making by animals of varied movements, which bring them into varied relations with the environment, until certain of these relations prove advantageous and therefore persist. To this way of acting, which has received various names, including (from the present reviewer) the unfortunately misunderstandable one of "method of trial and error," Zur Strassen gives the expressive name of the "shot-gun method." Some such evidently figurative term is doubtless its best appellation, as reducing the temptation to read higher things into it.

But now we come to the case of man; do our principles of interpretation exclude psychic factors here also? Most undoubtedly they do, if the reasoning up to this point has been well based. Greater complication there is, but no difference in principle; Zur Strassen sets forth that there is no reasonable ground for making a distinction between the behavior of man and that of animals in this matter. And so, are we led to the absurd conclusion that there are no psychic processes, no consciousness, in man?

Here we perceive that two questions must be distinguished—two questions which we shall try to formulate even more sharply than the author has done, because the usual failure to distinguish them has tremendously confused this whole matter. The questions are: (1) Does mind exist in men and animals? (2) Does mind play such a part in the behavior of men and animals that a complete objective explanation of the behavior can not be given without taking it into consideration?

To this second question Zur Strassen answers, No: a satisfactory explanation of the behavior of man and animals can be given without taking into consideration any factors but objective,

physico-chemical ones. But this has no bearing on the answer to the *first* question: it is no argument against the *existence* of mind in either man or animals, for it does exist in man. It may therefore exist in animals: the author concludes, as he is bound to, that the probability is that men and animals are alike in this matter; that animals also are conscious. His only contention is that mind is not a *factor* in determining objective behavior; or as the reviewer would prefer to put it, that a complete objective explanation of behavior can be given without taking into consideration consciousness.

Zur Strassen's discussion brings out two points that much need recognition. (1) If we adopt the principle of parsimony of explanation as a test for the *existence* of psychic qualities, as has been done by various authors, we inevitably come to the result that such qualities do not exist, even in places where we know, by direct experience, that they do exist. When I withdraw my burned finger from the flame, consciousness is no more required for an objective explanation of this action than it is for the withdrawal of Amœba under similar conditions, yet in my case there *is* consciousness, of a very intense character. Therefore the result of the application of this principle of parsimony is no test whatever for the existence of psychic qualities. A consistent carrying through of the principle places man and animals in the same category, and is therefore, as Zur Strassen maintains, rather favorable than otherwise, to the general distribution of consciousness in animals.

(2) Admission of the existence of consciousness in animals is not equivalent to holding that consideration of this consciousness is required for a complete objective explanation of behavior. This point needs to be sharply realized. Look at the matter experimentally. A complete explanation, from an experimental point of view, is one in which the preceding condition is shown to contain differential factors for determining all the differentiations of the succeeding condition. The question whether consciousness is a "factor" requiring consideration in objective explanations resolves itself experimentally into this: Do we sometimes, in analytical experimentation, come to situations where there are no differences in experimentally perceivable factors to account for differences in our results? If we could perceive accurately all the objective factors present, should we find that sometimes two identical combinations give different

results? If so we might be compelled to conclude that some factor x, not perceivable objectively—a psychic factor, perhaps—is playing a part. And this of course would mean the bankruptcy of the experimental method; it would mean that things happen which are not determined, so far as experiment can show; that when differing results appear in two cases, we cannot look with confidence for any antecedent differences in the conditions to explain them; that by supplying the same conditions in two cases we can not be sure of getting the same results; it would mean that nature plays fast and loose with us so far as objective experimentation is concerned. To the experimentalist the question whether states of consciousness may at times come in and alter his results, without the accompaniment of changed objective conditions to which the changed results can be attributed, is evidently an intensely practical one, and so long as this possibility is held open, it is idle to tell the experimenter that he should not concern himself about psychic processes.

But if, as is commonly held, states of consciousness are always accompanied by objective physiological conditions, and these objective conditions differ when the conscious states differ, then of course we should always be able to find satisfactory objective determining factors for all differing results; a complete experimental explanation of what happens could be given, without taking into consideration unknown states of consciousness; the objective experimental method would be reliable. There seems to be no convincing evidence as yet that it is not reliable and sufficient unto itself; it will be best to hold to it till such evidence appears. And yet, as we have seen, to hold to it as reliable and sufficient does not imply in the least that states of consciousness do not likewise exist.[1] Comparative psychology and a purely objective science of animal behavior, complete in itself, may exist side by side without the least conflict.

H. S. JENNINGS.

[1] It does not even imply, I believe, that consciousness is without effect on action. A good case could be made for the effectiveness of consciousness, in a widened experimental sense, even though a purely objective explanation, without gaps, can be given for behavior.

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